Status Review of the Eastern Oyster (*Crassostrea virginica*)

Report to the National Marine Fisheries Service, Northeast Regional Office, February 16, 2007

NOAA Fisheries Eastern Oyster Biological Review Team

U.S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

NOAA Technical Memorandum NMFS-F/SPO-88
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1 Executive Summary

NOAA's National Marine Fisheries Service (NMFS) received a petition to list the eastern oyster (*Crassostrea virginica*) as either threatened or endangered under the Endangered Species Act (ESA). Following a positive 90-day finding, wherein it was determined that the petition and the information in NMFS files contained substantial information indicating that the petitioned action may be warranted, a Biological Review Team (BRT) was convened to review the status of eastern oysters throughout their range.

During deliberations, the BRT met three times to analyze and summarize the available information on the status of this species. This document is the BRT's status review for the eastern oyster, as guided by the ESA. It presents a summary of published literature and other currently available scientific information regarding the biology and status of eastern oysters, as well as an assessment of existing regulatory mechanisms and current conservation and research efforts that may yield protection for the species.

As invertebrates, a listing determination for eastern oysters must be based on the species' status throughout "all or a significant portion" of its range. Eastern oysters are widely distributed along the East and Gulf coasts of the United States, and their range extends internationally into Canadian and Caribbean waters. Several recent genetic studies have been undertaken to better understand the population structure of *C. virginica,* and these studies have found strong patterns of differentiation on the basis of different sequencing data. Studies indicate to two separate populations, one within the Atlantic region and one within the Gulf of Mexico with an intermediate zone between these populations found on the eastern coast of Florida in the general area of Cape Canaveral.

Commercial landings throughout the species' range along the East Coast have declined to approximately two percent of the recorded historic highs. In the Gulf of Mexico, however, harvest has generally increased or remained stable in the last several years. Louisiana is now the top-producing oyster-state and has contributed an average of 42% of the total U.S. harvest. Fishery harvest declines, often cited as cause for alarm, are widely-recognized as unreliable indicators of population trends. Landings data are more a metric of fishery success rather than species abundance.

Oysters are considered a keystone species in most estuaries along the Atlantic and Gulf coasts, and self-sustaining populations play an essential role in the ecology of these estuaries. There are few data available regarding historic and current oyster reef acreage estimates, and available fisheries dependent and independent data are limited. In order to gather additional data to assess the status of the species, the BRT conducted a telephone survey of state resource managers and oyster experts. Respondents were asked to provide the following information for each estuary within their region/area: historic and current oyster acreage estimates, harvest rates and regulations, the sustainability of oyster populations with and without restoration, recruitment, and the primary threats facing oyster populations. Even though oyster harvests are at or near record low levels along the majority of the US Atlantic coast, resource managers and independent experts surveyed by the BRT indicated that overutilization (overharvesting) is currently a minor threat to oyster populations occurring only seven times out of the 286 threats listed for the 71 estuaries assessed by respondents. Information obtained through the survey also strongly suggests that recruitment is sufficient to maintain the viability of eastern oyster populations throughout the species' range except in a portion of the mid-Atlantic (e.g., Long Island Sound, Peconic Bay, Hudson-Raritan Estuary). Restoration and enhancement efforts for fisheries and conservation are occurring throughout the species' range, but are more common in the north and mid-Atlantic. In estuaries where restoration and enhancement efforts are occurring, they are considered necessary to sustain populations in roughly half of the estuaries in the mid and south Atlantic regions (presumably, to support commercially viable populations). In the North Atlantic (specifically, Connecticut and Rhode Island) and the Gulf of Mexico, restoration and enhancement efforts are not necessary to sustain biologically viable populations but are considered important to maintaining a fishery and conserving ecosystem services.

Restoration efforts for oysters are often motivated by interest in reclaiming ecosystem services and/or sustaining fisheries, not by a perceived need to protect the species itself. Domestication and farming of reproductively-isolated breeds of eastern oysters is expanding to satisfy market demand, with the ancillary benefit of moderating harvest pressure on natural populations.

Eastern oysters display a wide range of survival strategies. They are both colonizers and ecosystem engineers and have a high reproductive potential. The species' ability to adapt to a wide range of environmental conditions (e.g. tolerance for low dissolved oxygen and wide ranges in salinity and temperature) makes it resilient. Eastern oysters inhabit a naturally-variable environment, and evidence suggests that past local extirpations and colonizations have been common over geologic time. There are some threats that may be significant at a regional or local level. However, while the species encounters many threats throughout its range, none are considered to be overwhelmingly dominant or advancing at a rate that would threaten the viability of the species throughout its full range. Based on the available information, the BRT therefore concluded that the long term persistence of eastern oysters throughout their range is not at risk now or in the foreseeable future.

2 Introduction

2.1 General Introduction

NMFS received a petition from Mr. Wolf-Dieter Busch, Ecosystem Initiatives Advisory Services to list eastern oyster as either threatened or endangered under the ESA. Following NMFS' positive 90-day finding, wherein the petition was determined to contain substantial information, NMFS convened an eastern oyster BRT to review the status of the species concerned.

In order to conduct a comprehensive review, the BRT was asked by NMFS to assess the species' status and degree of threat to the species with regard to the factors provided by section 4 of the ESA without making a recommendation regarding listing. The BRT was provided a copy of the petition and all information submitted as part of the data request that was specified in the Federal Register Notice announcing the 90-day finding. The BRT reviewed all this information during its consideration and analysis of potential threats to the eastern oyster. This status review document is a summary of the information assembled by the BRT and incorporates the best scientific and commercial data available. In addition, the BRT summarized current conservation and research efforts that may yield protection, and drew scientific conclusions about the health of eastern oyster resources throughout the species' range.

2.2 <u>ESA Background</u>

The purposes of the ESA are to provide a means to conserve the ecosystems upon which endangered species and threatened species depend, to provide a program for the conservation of endangered and threatened species, and to take appropriate steps to recover a species. The U.S. Fish and Wildlife Service (USFWS) and NMFS share responsibility for administering the ESA; NMFS is responsible for determining whether marine, estuarine or anadromous species, subspecies, or distinct population segments are threatened or endangered under the ESA. To be considered for listing under the ESA, a group of organisms must constitute a "species."

The ESA provides the following definitions:

> *"the term **species** includes any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature."*
>
> *"**endangered species**" is defined as "any species which is in danger of extinction throughout all or a significant portion of its range."*
>
> "***threatened species**" is defined as "any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range."*

Additional criteria regarding entities appropriate for listing under the ESA have been set forth. First, there is the ability to identify and list distinct populations segments (61 FR 4722) or evolutionarily significant units (56 FR 58612) when a population satisfies the criteria of being discrete and significant; however, these policies are limited to vertebrates and therefore, are not within the scope of this status review.

The process for determining whether a species (as defined above) should be listed is based upon the best available scientific and commercial information. The status is determined from an assessment of factors specified in section 4(a)(1) of the ESA including:

- (A) The present or threatened destruction, modification, or curtailment of its habitat or range;
- (B) Overutilization for commercial, recreational, scientific, or educational purposes;
- (C) Disease or predation;
- (D) Inadequacy of existing regulatory mechanisms;
- (E) Other natural or manmade factors affecting the continued existence of the species.

Within this status review report (SRR), the BRT also summarized ongoing protective efforts to determine if they abate any risks to eastern oysters. When a species is listed as endangered under the ESA, it is afforded complete protection by the ESA, including the development and implementation of recovery plans, requirements that Federal agencies use their authorities to conserve the species, and prohibitions against certain practices, such as taking individuals of the species. Under NMFS policy, when a species is listed as threatened, the prohibitions for take are not automatically afforded. These prohibitions must be specifically afforded to a threatened species through a special rule (section 4(d) of ESA). Specifically, the prohibitions of section 9 of the ESA, in part, make it illegal for any person subject to the jurisdiction of the United States: to take (i.e., to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture or collect, or to attempt to engage in any such conduct); to import into, or export from, the United States; to ship in interstate or foreign commerce in the course of commercial activity; or to sell or offer for sale in interstate or foreign commerce any endangered wildlife. To possess, sell, deliver, carry, transport, or ship, endangered wildlife that has been taken illegally is also prohibited. However, section 10 of the ESA provides NMFS with the authority to grant exemptions to the section 9 taking prohibitions for scientific research, enhancement, and incidental take permits. The ESA provides some exceptions to the prohibitions, without permits, for certain antique articles and species held in captivity at the time of the listing. The ESA also provides for possible land acquisitions and cooperation with the states. In some instances, species that are not listed under the ESA are afforded protection. For example, Section 4(e) of the ESA, entitled "Similarity of Appearance Cases," allows the Secretary (of Commerce or Interior), by regulation of commerce or taking, to the extent he deems advisable, to treat any species as an endangered species or threatened species even though it is not listed if he finds that: (1) Such species so closely resembles a listed species in appearance, that enforcement personnel would have substantial difficulty in differentiating between the listed and unlisted species; (2) the effect of this substantial difficulty is an additional threat to an endangered or threatened species; and (3) such treatment of an unlisted species will substantially facilitate the enforcement and further the policy of the ESA.

2.3 The Petition

On January 11, 2005, NMFS received a petition from Mr. Wolf-Dieter Busch (the petitioner), Ecosystem Initiatives Advisory Services, to list eastern oyster (*Crassostrea virginica*) as threatened or endangered under the ESA. After reviewing the information contained in the petition and in our files, NMFS determined that there is sufficient information to indicate that the petitioned action may be warranted. On May 18, 2005, NMFS published a positive 90-day finding in the Federal Register. This initiated this status review process.

On Wednesday, October 19, 2005, NMFS received a letter from the petitioner dated October 13, 2005 requesting the recall of the eastern oyster petition. In his letter, the petitioner indicated that his request to withdraw the petition was due to the public and industry's confusion over the petition and listing process. He noted the significant concerns of some that the species may be listed as endangered; thereby, creating severe restrictions and regulations for this resource. He also expressed concern that given the timeline of the review, NMFS may not currently have enough information to determine if eastern oyster subspecies exist. He concluded that he hopes that NMFS will continue with the review as he considers the status review report to be a comprehensive resource which will be of great value in focusing restoration activities for this resource.

NMFS accepted this request and as a result, ceased the evaluation of the petition. However, a considerable amount of effort had been expended by the BRT at the point at which the withdrawal of the petition occurred. Also, the completed status review report is the most timely and comprehensive resource document for this species. As such, NMFS determined that because the report is a useful tool in guiding future management decisions, the BRT should complete the status review report.

3 Species biology

3.1 Life history

Morphology

The eastern oyster, *Crassostrea virginica*, (phylum Mollusca, class Bivalvia, order Ostreoid, family Ostreidae) is a monomyarian lamellibranch exhibiting bilateral asymmetry and a restricted coelom (Seed 1983). The foot and adductor muscle, present only during larval stages, is reabsorbed after metamorphosis resulting in the monomyarian condition (Kennedy 1996, Morrison 1996). Valves are asymmetrical with the left valve generally thicker and more deeply cupped than the right (Yonge 1960; Galtsoff 1964). When closed there is no gap between the two halves. Eastern oysters settle on the left valve leaving the right valve always on top.

Shell shape and thickness is variable and differs depending on the environment in which the oyster grows. Umbones are curved and point toward the posterior, and shells are thicker when growing on hard substrates. In silty environments or on reefs, umbones grow generally straight, but shells are more fragile than those growing on hard substrates. Solitary oysters found on hard substrates are usually rounded with radial ridges and foliated processes while those growing on soft substrates and reefs are more slender with few ridges (Stanely and Sellers 1986).

The interior of the shell has a prominent purple-pigmented adductor muscle scar located close to the dorsal end of the valve (Figure 1). The purple pigmentation of the adductor muscle scar differentiates the eastern oyster from similar species.

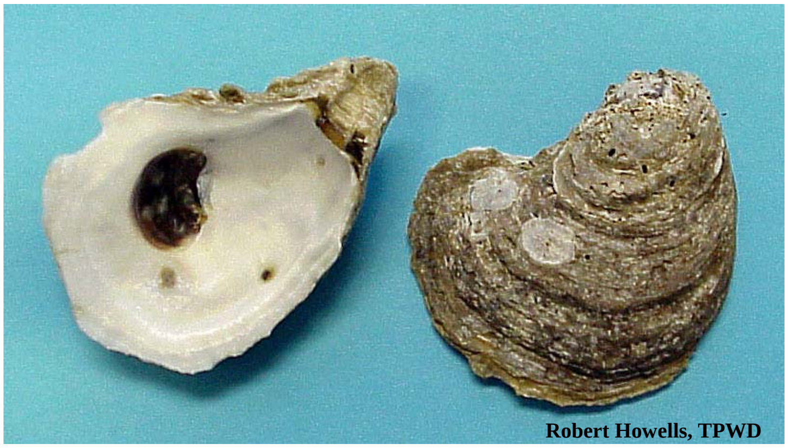

Figure 1. Eastern oyster, *Crassostrea virginica* (photo credit: Texas Parks and Wildlife Department)

Oysters exhibit great morphological plasticity as adults, but quite static morphology and behaviors as larvae. The former is due to tremendous environmental variability and lack of selection on adult form, and the latter is due to evolutionary forces constraining the single motile life stage upon which the species is dependent for long-term persistence in a highly variable and ever changing estuarine environment (Carriker 1996).

Reproduction

Eastern oysters are protandric, individuals first mature as males then typically change to female later in life, and there is also evidence suggesting that the process is reversible later in life (Thompson et al. 1996). The factors determining sex are varied and complex. Oysters may also change sex annually in response to environmental, nutritional and/or physiological stresses (Tranter 1958 cited by Thompson et al. 1996; Bahr and Hillman 1967; Davis and Hillman 1971; Ford et al. 1990). Other studies suggest that sex determination may be influenced by the sex and proximity of nearby oysters (Needler 1932; Burkenroad 1931; Smith 1949; and Menzel 1951 all cited by Thompson et al. 1996). In Canada, few males changed sex when in close proximity to females (Needler 1932 as cited in Thompson et al. 1996). Burkenroad (1931) found a higher ratio of females to males in >4 cm oysters growing unattached and an equal distribution for smaller oysters growing in clumps in Louisiana. In South Carolina, sex ratios were skewed toward more males when growing in aggregate as opposed to those growing singly (Smith 1949 as cited in Thompson et al. 1996). Experimental studies in Chesapeake Bay, Maryland showed that approximately one-third of single sex oysters had changed to the opposite sex when held in trays over the winter (Kennedy 1983). Thompson et al. (1996) noted that sex reversal usually occurred between spawning seasons when the gonad was undifferentiated.

Fecundity is difficult to determine in oysters due to a prolonged spawning period with intermittent spawning and redevelopment throughout the year and gonadal tissue that is diffuse and integrated into surrounding tissue (Thompson et al. 1996). However, estimates range from 2 to 115 million eggs per female, depending on size and geographic location (Galtsoff 1930, 1964; Davis and Chanley 1956; Cox 1988; Cox and Mann 1992; all cited in Thompson et al. 1996).

Spawning is initiated by a combination of factors including water temperature, salinity and physiochemical interactions (Galtsoff 1964; and Loosanoff 1953 cited by Berrigan et al. 1991; Hayes and Menzel 1981; Hofstetter 1977, 1983). Spawning is seasonal (summer) throughout the mid to northern Atlantic portions of the species' range. In southern waters spawning occurs in all but the coldest months (Berrigan et al. 1991). Conditions generally required for spawning include water temperatures at or above 20° C and salinity higher than 10 practical salinity units (psu). When these conditions persist, spawning can continue year-round (Breuer 1962).

Larval Phase

After fertilization, oysters develop through several free-swimming larval stages before attaching to a hard substrate and becoming sessile. The rate of development through these stages is highly temperature dependent (Shumway 1996). The mechanisms for larval dispersal and recruitment are still unclear (Epifanio 1988). Larval retention is generally explained by "passive" transport induced by physical factors, by an "active" process involving larval swimming, or by a combination of both (Dekshenieks et al. 1996). The first larval stage (trochophore) is formed four to six hours following fertilization and lasts approximately one to two days. The trochophore larva does not feed, but subsequent larval stages (veliger) are planktotrophic, feeding on small plants and animals (Kennedy 1996). Veliger stages, lasting up to two months (Hopkins 1931), include several morphological changes to the larvae resulting in a fully developed larva possessing a well-developed foot. The foot is used for locomotion when seeking a place to attach after settling on appropriate substrate and is reabsorbed upon final metamorphosis into an attached oyster.

As oyster larvae become competent to settle they must locate a suitable substrate upon which to attach. Larvae may exhibit exploratory behavior in locating a suitable substrate upon which to settle (Burke 1983 as cited in Kennedy 1996). Both environmental and internal cues are used in determining when and where veliger larvae will settle (Kennedy 1996). Settlement is a behavioral response that can be repeated or reversed and is followed by metamorphosis, which results in morphological changes and is permanent (Kennedy 1996). There is evidence that suggests metamorphosis is initiated (triggered) by salinity and by chemicals given off by live oysters and bio-films on other suitable substrates (Hidu and Haskin 1971, Keck et al. 1971; Kennedy 1996). Larvae appear to exhibit negative phototaxis, a preference which suggests that habitats with complex interstitial spaces may provide better habitat for settlement. The process of settlement, metamorphosis, and attachment normally occurs two to three weeks after hatching, but can be delayed for up to a month or longer depending on environmental conditions (Stallworthy 1979 as cited by Kennedy 1996; Kennedy 1996).

Environmental Tolerances

Temperature, salinity and food availability greatly influence oyster growth, and therefore, rates vary seasonally at a given latitude with maximum growth occurring during the summer and fall. The minimum temperature reported for growth of oyster larvae was 17.5º C (Hofstetter 1977). Eastern oysters have been reported to survive freezing temperatures in shallow-water habitats and after being exposed to temperatures in excess of 45º C in intertidal areas (Galtsoff 1964; Shumway 1996). However, exposures to temperatures above approximately 35º C will adversely affect pumping rate and thereby feeding (Loosanoff 1958; and Galtsoff 1928 as cited by Shumway 1996). Growth of oysters in the higher latitudinal regions stops or slows during winter (Loosanoff and Nomejko 1949). Oysters are capable of growth throughout the year in the Gulf region but optimum temperatures range from 20 to 30º C (Stanley and Sellers 1986).

Oysters can tolerate salinities from 0 to 42 psu, but the optimum range is 14 to 28 psu (Quast et al. 1988; Shumway 1996). A minimum salinity of 10 psu is required for growth with little growth occurring at salinities less than 5 psu (Shumway 1996). Viable, reproducing populations of oysters have been found to persist off the mouth of the Atchafalaya River in Louisiana where salinities sometimes are less than 5 psu for several months (pers. comm. Banks 2006). Mortalities usually only occur when water temperatures exceed 30º C in the summer (pers. comm. Banks 2006). There is some evidence that suggests the effects of high water temperature are exacerbated by low salinity events resulting from heavy rainfall freshets (Shumway 1996).

Growth and Feeding

Growth rate is highly dependent on temperature and food supply (Kennedy 1996). Oysters undergo rapid growth (reaching 10 mm month^{-1}) during the first six months of life but slow throughout the rest of their life (Quast et al. 1988) reaching approximately 15 cm in five or six years (Hofstetter 1962; Berrigan et al. 1991). Harvest size (76-90 mm) is reached in the Gulf of Mexico 18-24 months after setting (Hofstetter 1977; Berrigan et al. 1991) whereas oysters from Long Island Sound take 4-5 years to reach a similar size (Shumway 1996). Shell growth is not uniform between the two valves with the left valve growing faster than the right (Carriker 1996).

Oysters continue to grow throughout their life though the rate diminishes with age (Carriker 1996). Maximum size can be up to 20.6 cm (Boothbay Harbor, Maine; Galtsoff 1964) to 35.5 cm in the northeast (Damariscotta River, Maine; Ingersoll 1881 as cited in Carriker 1996). In the Gulf of Mexico, eastern oysters have been found to live 25-30 years and reach sizes to 30 cm (Martin 1987). These large individuals are usually associated with undisturbed bottoms where commercial fishing is prohibited and (Carriker 1996).

Oysters are filter feeders, feeding primarily on phytoplankton and suspended detritus (Langdon and Newell 1996). Food items range in size from 1-30 µ (Mackie 1969; Quast et al. 1988; Newell and Langdon 1996). Clearance or filtration rates have been reported to range from 1.5-10.0 L $h^{-1}g^{-1}$ dry tissue weight (Stanley and Sellers 1986; Newell and Langdon 1996). *Crassostrea virginica* are capable of adjusting feeding rates depending on the size, type and composition of the available food source (Baldwin 1995, Baldwin and Newell 1995a, 1995b as cited in Kennedy 1996).

Langdon and Newell (1996) note there is no evidence to suggest that oyster larvae are food limited in the wild while other studies have shown that oysters consuming low protein food sources had better growth rates than those exposed to high protein food sources (Flaak and Epifanio 1978; Utting 1986; both cited by Langdon and Newell 1996). As sessile, non-motile organisms, oysters must rely on food-laden water being moved past the oyster in order to extract food from the water column. Water flow across oyster reefs has been shown to influence growth rate (Newell and Langdon 1996). Excessive water flow causes food particles to move through the area before they can be extracted from the water column (Newell and Langdon 1996); too slow and there are not enough food particles available to support growth (Grizzle et al. 1992 as cited by Newell and Langdon 1996). Optimal growth is a function of multiple interactions of environmental factors and food availability (Loosanoff and Nomejko 1949, Shumway 1996).

Habitat preference

While oysters are capable of surviving in a wide range of habitat conditions, the preferred habitat (general range) conditions in areas where eastern oysters are common, based largely on Shumway (1996) and Hargis and Haven (1999) and others as noted, are considered to be:

Depth- 0.6-2.0 m (range 0-11m) in Canadian waters (Jenkins et al. 1997); mostly between 0.6-5.0 m in Mid-Atlantic States waters (MacKenzie 1996) although oysters occur commonly inter-tidally south of Maryland (Burrell 1997) and in deeper waters in some areas, e.g., to 8 m in Chesapeake Bay (MacKenzie 1997a); 0.0-4.0 m in Gulf of Mexico (MacKenzie and Wakida-Kusunoki 1997; Dugas et al. 1997).

Salinity-larvae (10-27.5 ppt; 17.5 ppt optimum for Long Island Sound stock (Calabrese and Davis 1970)), adults (normally ~5-40 ppt),

Temperature- larvae (optimum ~20.0-32.5ºC) (Calabrese and Davis 1970); adults optimum temperatures range from 20 to 30ºC (Stanley and Sellers 1986) , survival under extremes from -2 to 36 ºC, and to 49ºC for short periods of time)

Substrate- larvae (clean hard or shell substrate), adults (various substrates, including mud, that support their growing or accumulative community weight) (Jenkins et al. 1997)

Geomorphology- sheltered drowned river valleys and bar-built lagoonal estuaries (MacKenzie and Wakida-Kusunoki 1997)

pH- larvae, normally 6.75-8.75 (Calabrese and Davis 1966)

Tidal range- 0.5 m (in restricted lagoons or upper estuaries) to 2.7 m (Gulf of St. Lawrence; Jenkins et al. 1997)

DO- ~20-100% saturation

Hydrographic circulation- such as to cause oyster larvae to remain near existing reefs but with enough exchange to maintain a good food supply and near neutral silt balance on the oyster reefs/beds (Lenihan 1999). Sensitivity analyses of some bivalve populations suggest that their population stability and growth rates are more sensitive to changes in larval survival and recruitment than they are to adult survivorship or fecundity (Brousseau 2005), except perhaps when disease (parasite) infection rates are high.

3.2 Ecology and Population Dynamics

The eastern oyster is a remarkably resilient species in the dynamic physical environment of intertidal and near-shore estuarine ecosystems. This resilience can be attributed, at least partially, to an unusual combination of characteristics. The oyster is both a “colonizer” and an “ecosystem engineer.” Species that are colonizers tend to be highly fecund with wide distribution of offspring; they are often the first organisms to occupy new niches opened by changes in the physical environment. Ecosystem engineers modify the physical environment to make it more suitable for long-term survival; they create their own niches. The reef-building capabilities of oysters qualify them as ecosystem engineers; accumulation of shell ensures a substrate for future generations to occupy and also accomplishes genetic mixing between generations – older oysters can mate with younger – thereby conserving genetic diversity. This combination of colonizing and engineering capabilities has allowed the oyster to persist in the highly-dynamic environment of coastal seas and estuaries, re-colonizing areas impacted by storms and other physical displacements and moving with the rise and fall of sea level (Dame 1993, 1996).

Recruitment

While the mechanisms of dispersal and recruitment are still unclear (Epifanio 1988), there remains considerable spatial and temporal variability in both seasonal and local recruitment patterns. Nutritional and reproductive stress has been implicated in explaining some of this variability (Nelson 1905, Helm et al. 1973, both cited in Kennedy 1996). Estuaries subjected to high tidal-flushing activities tend to have low, but consistent recruitment intensities while those with low freshwater inflows and sluggish circulation allow for extended residence-time for larvae and higher but irregular recruitment (Kennedy 1996). Larval retention is generally explained by 'passive' transport induced by physical factors, by an 'active' process involving larval swimming, or by a combination of both (Dekshenieks et al. 1996). Differential recruitment patterns on a microhabitat scale have also been identified though the causes are yet undetermined (Kennedy 1996). Mortality rates are more sensitive to changes in larval survival and recruitment then they are to adult survivorship or fecundity (Brousseau 2005), except perhaps when disease-parasite infection rates are high.

Ecological Role

Oysters are an ecological keystone species in most estuaries along the Atlantic and Gulf coasts. Oyster populations contribute to the integrity and functionality of estuarine ecosystems. Self sustaining oyster populations form reefs that 1) contribute to trophic dynamics by promoting species diversity; 2) provide structural integrity that supports community stability, enhances habitat values and affects water circulation and flow patterns; and 3) perform ecological services which improve water quality and recycle nutrients.

Water Filtration

Clearance rates (volume of water totally cleared of suspended particles per unit time) for adult oysters have been reported as high as 10 L $h^{-1}g^{-1}$ dry tissue weight (Jordan 1987 as cited in Newell and Langdon 1996). Pseudofeces, physiologically defined as consisting of particles that have been trapped (filtered by gill cilia), combined with mucous, transported toward the mouth, but rejected by the palps prior to being ingested (Barber 2006), are a significant source of sediment on reefs and in areas of little water movement can quickly smother live oysters (Lund 1957). Due to the high clearance rates of eastern oysters they are being evaluated as a possible bioremediation tool to reduce contaminant loading in marsh-estuarine systems (Breitburg et al. 2000).

Reef Habitat Creation

Oyster reefs provide valuable refuge, trophic support and complex structure for a variety of juvenile and adult finfish and are considered essential fish habitat for managed and unmanaged species (Coen et al. 1999, SAFMC 1998, GSMFC 2004). Oyster reefs may function similarly to submerged aquatic vegetation in regions where seagrasses are not abundant. For example, in some Texas bay systems spotted sea trout and red drum utilize oyster reefs as foraging areas while seagrasses are used in a similar manner in other ecosystems (Holt and Ingall 2000).

Bahr and Lanier (1981) documented over 40 macrofaunal species or groups that live on oyster reefs while the total number of species in an oyster community have been identified in excess of 300 (Wells 1961). Motile arthropods such as crabs (Xanthidae), snapping shrimps, isopods and amphipods, polychaetes (e.g. Nereidae, Syllidae), gastropods such as the oyster drill (*Stramonita haemastoma, Urosalpinx cinerea*) as well as sessile invertebrates such as mussels, chitons, limpets, barnacles, anemones, bryozoans, hydroids, and sponges may be found in oyster reef habitat. Suspension and deposit feeding activities provide trophic support for higher consumer levels by converting detritus to animal biomass and to primary producers through mineralization of carbon and release of nutrients such as nitrogen and phosphorous (GSMFC 2004).

Oyster reef configurations are highly variable in both shape and size, ranging from small mounds or patch reefs to long, wide ridges that may extend for miles. In soft sediment environments oyster reefs can serve to reduce erosional processes as constructed reefs in Louisiana showed the potential to reduce adjacent shoreline erosion at low-energy locations (Piazza et al 2005). Reefs may ultimately divide bays and change circulation patterns (Diener 1975) thus altering local environments and the associated flora and fauna (Britton and Morton 1989). High density oyster communities occur in areas where water currents are high enough to supply food to many individuals yet low enough to limit turbidity from re-suspending sediments (Britton and Morton 1989).

In the northern part of the range, winter freezing limits intertidal survival; therefore, oysters are limited to subtidal environments. Growth rates are limited by temperature, and predators tend to have a large impact on survival. Thus, oysters are found in subtidal beds at modest densities that mitigate predation, but still permit effective spawning. Recruitment tends to be periodic (Kennedy 1996). In these environments, natural oyster populations tend to include several generations in long-lived, low-relief beds. As many of these beds have been harvested to a point where extracting more oysters from them is no longer cost-effective, most oyster production in the northeast is based upon aquaculture (MacKenzie 1997a).

In the mid-Atlantic region, high-relief oyster "reefs" once kept oysters in the upper levels of the water column where phytoplankton densities are high and hypoxia is rare (Lenihan and Peterson 1998). However, remaining reefs are mere footprints of the original structures that were removed by decades of harvest (Rothschild et al. 1994; McCormick-Ray 1998; Haven and Whitcomb 1983; Hargis and Haven 1999; Jackson et al. 2001). In these ecosystems, parasitic diseases often limit survival, and growth may be temperature or food-limited.

Toward the southeast Atlantic and into the Gulf of Mexico, oysters are rapid colonizers and occur in abundance in the intertidal zone. However, many northern Gulf of Mexico populations are located subtidally. Growth rates, among intertidal populations are limited by feeding, but reproduction, fecundity, and recruitment may be extremely high. Oyster also occur in abundance on subtidal reefs where pests and predators (shell-boring sponges, rays) may negatively affect survival, but warmer winter temperatures and the year-round growing season act to enhance survival.

3.3 Distribution

Historic Distribution

According to Hargis (1999) and Steimle (2005), during the last ice age, sea levels were about 100 m lower than present times and most of the proto-estuaries as well as now nonexistent estuaries were located further offshore on the Atlantic and Gulf of Mexico continental shelf. Where environmental conditions allowed, the eastern oyster inhabited these proto-estuaries. As sea level rose these estuaries and the oysters moved inshore and came to occupy the submerged river valleys and coastal areas recognized as today's estuaries, or new estuaries were created via barrier beach-lagoon formation.

In the Northeast, where the glaciers covered the land from Staten Island NY to Cape Cod, Massachusetts, and perhaps to Georges Bank, the adjacent dry continental shelf was like an artic tundra and probably any ice free estuaries were inhospitable to marginal for the oyster, except at the very outer edge of the continental shelf due to the influence of the Gulf Stream. At that time, Georges Bank was an island and possibly connected to Cape Cod. Other areas that are now submerged shoals in the Gulf of Maine and off Nova Scotia were also islands and potential oyster habitat. As glaciers retreated and melted, the sea level rose as did coastal water temperatures. About 8000 years before present (YBP) there is evidence that there were oysters living on the shelf on the inwardly moving proto-estuaries (Merrill et al. 1965). About this time they might have entered the current Chesapeake Estuary System (Hargis 1999) and slightly later the Hudson-Raritan system as evidenced from radiocarbon dating of oyster shell collected on the mid-continental shelf and within the estuaries.

In the Hudson River, there is evidence to suggest oyster populations established themselves initially about 7000 YBP in the Tappan Zee area. Oyster populations may have retreated down stream for a time with climate and rain fall cycles. Newly uncovered fossil oyster reefs in the downstream area were also radiocarbon dated to this time, a dating that seems connected with the first American shell middens in the area. The radio-carbon dated shell deposition in the middens had gaps of several thousand years suggesting a partial loss of the resource in the downstream area.

When each Gulf and Atlantic estuary stabilized to near its current form oyster distribution might have varied. For example, Long Island Sound was a post-glacial, fresh water lake for a while until possibly a combination of sea level rise and fresh water rise breached the glacial moraine dams at both ends, so oysters could not enter that estuary until after the breach-conversion. There are data to suggest that temperatures rose quickly and that about 7000-8000 YBP sea level may have been near or slightly higher than present, providing an opportunity for the rapid northerly expansion of the species. However, there were also mini-ice ages, the most recent lasted until about the 18th century, where estuarine temperature might have declined to marginal levels for oysters in the northern portion of the species' range. Thus, the pre-colonial historic distribution of the eastern oyster within many Atlantic-Gulf estuaries may have been variable at time scales of decades to thousands of years, most likely responding to climate and water flow changes and occasional catastrophic events, such as major hurricanes.

Current Distribution

The eastern oyster occurs naturally in a great diversity of habitats along the western Atlantic Ocean from the Canadian Maritime Provinces to the Gulf of Mexico, Panama and the Caribbean Islands (Carlton and Mann 1996; Abbott 1974; MacKenzie 1997a; Jenkins et al., 1997; FAO 1978). *Crassostrea virginica* has also been described from Panama, Venezuela, Brazil and Argentina along the Caribbean Sea and the western Atlantic Ocean in Central and South America (Wallace 2001). Carriker and Gaffney (1996) report eastern oysters are distributed in the western Atlantic from Brazil northward through the Caribbean, and Gulf of Mexico to the St. Lawrence River estuary in eastern Canada, a range of some 8,000 km. Harry (1985) suggested that names of all populations of this species, such as *C. brasiliana*, *C. floridensis*, *C. guyensis*, *C. lacerata*, *C. rhizophorea*, and others should be replaced by *C. virginica*. However, Gaffney (Pers. Comm. 2005) now reports that the southern distribution of *C. virginica* can only be verified genetically to the northern Yucatan Peninsula of the Gulf of Mexico at present, and other genetically distinct *Crassostrea* species might occur in the Caribbean.

Eastern oysters have been transplanted outside of the species natural range. Ruesink et al. (2005) listed many transplanted *C. virginica* populations that have appeared to have survived to present in the areas to which they were transplanted or continue in mariculture operations. According to Ruesink et al. (2005), surviving, out-of-range *C. virginica* transplantations (with source in parenthesis) are found in: western Canada (North American east coast, since 1883); western US (US east coast since 1860s); western Mexico (unknown); Hawaii (unknown, since 1860s); Fiji (from Hawaii, 1970); Tonga (US west coast, 1973); Japan ("USA", 1968); Mauritius-Indian Ocean (US west coast, 1972); and possibly England (North American east coast, since 1870s).

3.4 Historic and Current Abundance

At the time of European colonization and the beginning of the localized heavy exploitation of the oyster for diverse purposes, oysters were reported from almost all estuaries along the Atlantic and Gulf coast. However, information on specific abundances within estuaries were often vague (Ingersoll 1881), especially beyond United States borders and in areas with low human population density and areas without active fisheries.

One confounding factor in understanding the full pre-European colonization distribution and abundance of the eastern oyster is that only shell remains are often available as evidence. Historic shell relics of the presence and distribution of the putative "eastern" oyster are apparently unreliable to define species distributions within the morphologically plastic and environmentally adaptive *Crassostrea* genus. This is especially problematic in the Gulf of Mexico and Caribbean (Gaffney Pers. Comm. 2005), which lead to the confusion over the species distribution described above.

Another confounding factor in understanding the recent, i.e., last ~150 yr, historic abundance of oysters is the lack of reliable quantitative survey data in many areas. Some current students of the species and fishery strongly contest earlier published estimates of abundances and local distributions (Kraeuter Pers. Comm. 2005). Kraeuter suspects that these estimates or area coverage of specific oyster beds or reefs might be overestimates by 80-90% in some areas.

These early surveys were focused on harvestable beds and often included natural, cultured or transplanted beds which may not have been well differentiated. Since the 1830s, the transplanting and movement of oysters for better growth has confounded understanding the natural abundance and local distribution of the species in many estuaries.

Abundance of the eastern oyster is known to have varied or declined in many estuaries in which it was previously known to be abundant. In some estuaries, abundance has declined due to one or more of the threats discussed below. Some populations have declined to the degree that they are defined as "ecologically extinct" no longer acting as a keystone species and providing ecosystem services to the estuarine ecosystem (e.g., the Hudson-Raritan Estuary). However, even in these locations, with effort, oysters can be found. The oyster can be found as isolated individuals or clusters even in unlikely urbanized places, such as the Hackensack River, Arthur Kill, Harlem River, East River and the Bronx River (Steimle 2005). However, these isolated survivors may currently exist at the thinnest of margins even though habitat quality has measurably improved and is currently suitable for good growth, as evidenced by oyster culturist results in this estuary complex.

The persistence of oysters in isolated areas at low abundance for perhaps decades, is not uncommon. Some local populations are now too widely dispersed to support enough successful spawning-fertilization and recruitment for natural repopulation (Pers. Comm. Luckenbach 2005). The low abundance situation of the Hudson-Raritan area may exist in other urbanized estuaries where oyster population surveys have not been done for decades. Some shellfish surveys were conducted without proper oyster sampling gear and focus because the oyster was not considered part of a useful or manageable fishery resource any more. Also, local management agencies may not want the fact that oysters still exist in areas to be generally known to avoid potential public health consequences because of bacterially contaminated water.

The notable decline of the oyster abundance distributions from estimated historic abundance distribution levels seems to be most prevalent in the more urbanized northeast, e.g., Chesapeake Bay, the Hudson-Raritan Estuary, southern Long Island NY, and some New England estuaries. However, most of the data to document this decline comes from fishery-dependent sources, which is somewhat controlled by socio-economic, not ecological, factors (MacKenzie 1996). This information base may not present an accurate picture of the abundance and status of oyster populations in many areas. The oyster distribution abundances south of Chesapeake Bay seem relatively stable, despite occasional major disturbances, such as hurricanes, based upon numerous southern Atlantic/Gulf Coast state reports presented during and after the congressional hearing on this issue (Marsh 2004; Perret 2005).

Biological (non-fishery resource focused) surveys have not yet been conducted with appropriate sampling gear and at appropriate levels of intensity according to a statistically reliable survey designs in areas where oysters previously existed or might still exist at reduced levels. However, methods and gear are available to do so (Chai 1992; Jordan et al. 2002). Due to the lack of surveys, we may not have an adequate understanding if the oyster has been extirpated from any ecologically significant areas.

3.5 Population Genetic Structure

Overview of Genetic Markers

There is a significant amount of literature on the use of genetic data to delineate taxa at various levels such as species, subspecies, and populations. Genetic data are also commonly used to understand a taxon's history in relation to geography, in a field of study known as phylogeography. As genetic techniques and markers continue to be perfected and additional ones are developed, these genetic tools are increasingly being applied to practical issues associated with the conservation of biological diversity. This section provides a basic overview of some of the most common types of genetic markers used today, the forces that operate on the genome to determine patterns of genetic differentiation, the general classes of data obtained from genetic markers, and the nature of inferences that can be drawn from these data.

Several different types of commonly used genetic markers are:

- *Allozymes* are products of alternative alleles at a locus (site on the DNA sequence) encoding for a specific enzyme. Because allozymes are functional proteins, they can be subject to selection.
- *Nuclear DNA* (nDNA) is located in the cell nucleus. It is inherited from both parents with recombination.
- *Mitochondrial DNA* (mtDNA) is located in the cell mitochondria. It is inherited as a single, non-recombinant genetic unit from the mother. Because of its clonal inheritance, mtDNA sequences can be used to trace maternal lineages across generations.
- *Microsatellites* are tandem repeats of 2-10 base pair nucleotide sequences. These sequences are often highly variable in the numbers of repeats they contain, and they are usually non-encoding.
- *Restriction fragment length polymorphism (RFLP)* is a method that examines genetic variation in lengths of DNA, either mitochondrial or nuclear, that result when the DNA is cleaved by restriction enzymes.
- *Denaturing Gradient Gel Electrophoresis (DGGE)* and *Single-Strand Conformational Polymorphism (SSCP)* are methods that detect variations in genetic sequences.
- *Single Nucleotide Polymorphism (SNP)* is a type of DNA sequence variation in which a single nucleotide (A, T, C, G) at one sequence position is altered.

The forces of genetic drift, gene flow, mutation, selection, and geographic history continuously act upon genomes. The effect of these forces on a particular genetic marker must be carefully considered in the interpretation of genetic data.

- *Genetic drift* is a passive process whereby allele frequencies change over time due to chance sampling events in the population. Populations with a large effective population size (N_e) exhibit slower rates of genetic drift than populations with small N_e. Also, mtDNA drifts more rapidly than nDNA because the effective population size of mtDNA is smaller by virtue of its maternal-only inheritance.
- *Gene flow* is essentially "effective" migration (m), and is dependent upon the number of successful (i.e., reproducing) migrants moving between populations each generation. Gene flow is estimated as N_em. Genetic differentiation of populations is highly sensitive to gene flow.

- *Mutation* occurs at different rates in different portions of the genome. At one end of the spectrum, genetic markers with extremely high mutation rates can become saturated with change upon change over time. At the other extreme, parts of the genome with extremely low mutation rates are evolutionarily conservative and show little to no differences among even distantly related taxa.
- *Selection* can act directly on a particular genetic marker, or on genetically linked loci. A strategy for ruling out the effects of selection upon a particular genetic marker is to examine multiple, independent (unlinked) loci.
- *Geographic history* involves the changes that result in the formation of geographic barriers or connections among populations.

The type of information provided by a genetic marker depends upon whether it provides frequency data or identity (sequence) data. *Frequency data* are characteristic of populations, not individuals. For example, individuals have alleles and populations have allele frequencies. Inferences from frequency data require several assumptions, including selective neutrality of the marker and equilibrium between mutation, gene flow, and drift. Frequency data are obtained from allozymes, microsatellites, and RFLPs. *Identity or sequence data* result from mtDNA or nDNA sequences, and are characteristic of individuals. Sequence data can be used to infer phylogenetic relationships among sequences, resulting in gene genealogies or "family trees." Also, sequence data can often provide insight into population structure not available from frequency data. For example, sequence data are often better than frequency data for teasing out the effects of geographic history.

The interpretation of genetic data is a rich field of study that continues to advance rapidly and cannot be summarized simply. As more genetic markers are developed and examined, our ability to unravel the origins and relationships among taxa increases in power and resolution. Along with these advances come challenges, one of which is to understand what it means when genetic markers applied to the same populations yield conflicting results. Such conflict does not imply that the genetic markers are flawed or unreliable. Nor does it mean that one of them is "right" and the other is "wrong." What it means is that they each have their own interpretation, each marker has been uniquely influenced by past experiences (i.e., the forces of genetic drift, gene flow, mutation, selection, and history), and some interpretations are just more detailed than others. As a rule, a finding of genetic differentiation is a strong conclusion, even if the reason for the differentiation is unclear. In contrast, a lack of differentiation is an ambiguous result which could be due to any one of several quite distinct factors (e.g., balancing selection, continued gene flow, no gene flow but insufficient time since separation for differentiation to occur).

Application of Genetic Markers to *C. virginica*

Based on the previous section, it is understandable that some populations that appear identical or homogenous on the basis of one genetic marker may later be found to be sharply differentiated by the application of another genetic marker. This is the case for *C. virginica* which has an extended pelagic larval stage that spans several weeks, and therefore, dispersal along the eastern coast was initially assumed to be extensive. In addition to a long pelagic stage, movement of oysters within their range and beyond was a common practice from as far back as the 1800's. At that time, transfers were made from the waters of the Chesapeake Bay to New England and eventually from the Carolinas to the Chesapeake once local populations diminished. In the 1960's, stocks from the Gulf of Mexico were brought into the Chesapeake to replenish local populations that were declining due to MSX (Carlton & Mann 1996). With such high levels of human-mediated movement, it seemed likely that high levels of gene flow would be exhibited all along the range of *C. virginica*.

As expected from the assumption of high gene flow, populations of *C. virginica* were initially found to be homogenous in allozyme frequencies across a large portion of the species range. An early allozyme study by Buroker (1983) provided evidence of a uniform population from Cape Cod to Corpus Christi using 32 allozyme loci, which exhibited genetic similarities among populations estimated to be 99% (Figure 3,4, & 5). However, allozymes can be less variable than other types of genetic markers (e.g., DNA sequence data) because allozymes represent variations in the amino acid sequence comprising a protein. Variation at the amino acid sequence level may mask underlying genetic variability at the DNA sequence level. Proteins usually have important biochemical functions so they could be strongly constrained by natural selection, acting to preserve protein functionality. Furthermore, a later re-analysis of Buroker's allozyme dataset by Cunningham and Collins (1994) revealed genetic structure not detected in the original analysis.

With time, more genetic studies were undertaken to better understand the population structure of *C. virginica*. These subsequent studies found strong patterns of genetic subdivision, with congruence among several different genetic markers indicating two separate populations: an Atlantic population and a Gulf of Mexico population with an intermediate zone between these populations located on the eastern coast of Florida.

Atlantic and Gulf Populations

RFLP studies of the entire mitochondrial DNA (mtDNA) of oysters from the Gulf of St. Lawrence to Brownsville, TX (Figure 2,4, & 5) by Reeb and Avise (1990) found two distinct (Atlantic and Gulf) genetic groups (genetic divergence level $p = 0.026$). West Palm Beach, Florida appeared to be a transition zone between the two populations with haplotypes from both groups found at intermediate frequencies. Based on the data, Reeb and Avise (1990) estimated that separation of the two populations occurred 1.2 million years ago. RFLP studies were also undertaken by Karl and Avise (1992) on single copy nuclear DNA (scnDNA) and found a similar genetic pattern with two distinct populations (Gulf and Atlantic) and an intermediate zone on the eastern coast of Florida (Stuart, FL- about 40 miles north of West Palm Beach) (Figure 3, 4, & 5).

Discrepancies between mtDNA RFLP data (Reeb & Avise 1990) and allozyme data (Buroker 1983) could be due to directional selection in the mitochondrial haplotypes observed or the smaller effective population size for mtDNA (as they are maternally inherited) which creates a faster rate of genetic differentiation (Karl and Avise 1992). Either hypothesis could be true if it were not for the nuclear RFLP data of Karl and Avise (1992) also running counter to the allozyme data. More likely balanced selection of the allozyme loci assayed or slower rates of evolution at the protein level may explain these discrepancies (Karl and Avise 1992). Subsequent reanalysis of Buroker's data by Cunningham and Collins (1994) found geographic structure within the allozyme dataset. However, that structure shows a peninsular Florida group clustering with an Atlantic group, which is incongruent with geographic population boundaries found in nuclear and mitochondrial RFLP studies.

Small and Chapman (1997) also looked at mtDNA to determine population structure of *C. virginica* but focused exclusively on RFLP analysis of the amplified portion of the mitochondrial 16s ribosomal gene. No population structure was found between oysters from Pamlico Sound, NC; Chesapeake Bay; and Galveston Bay, TX (Figure 3 & 5) which may be indicative of slower evolution rates at the 16s locus opposed to the rest of the *C. virginica* mitochondrial genome. Milbury et al. (2004; Figure 3) also looked at the mitochondrial 16s ribosomal gene but used Single Nucleotide Polymorphism (SNP) analysis to successfully differentiate between Gulf oysters planted in the Chesapeake Bay from local Bay oysters. The discrepancy between the two 16s studies may be due to a higher level of conservation around certain restriction enzyme sites on this particular locus opposed to SNPs which may not be as conserved. Wakefield and Gaffney (1996) found enough sequence variation at the 16s locus by denaturing gradient gel electrophoresis (DGGE) and direct sequencing to reveal three haplotypes that corresponded to the Gulf of Mexico, the South Atlantic, and the North Atlantic (Figure 3, 4, & 5).

Hare and Avise (1996) amplified the mitochondrial restriction site polymorphisms (RSP) found in Reeb and Avise (1990) for *Bst*NI and found a pronounced genetic cline along the eastern coast of Florida. Amplification of RSPs from the scnDNA loci from Karl and Avise (1992) also found a similar genetic pattern with the frequency of all Atlantic alleles (nuclear as well as mitochondrial) dropping 50-75% over the distance of 20 km between Oak Hill and Merritt Island (near the vicinity of Cape Canaveral) (Figure 3, 4, & 5). Hoover and Gaffney (2005) amplified four nonanonymous nuclear loci from individual samples from Prince Edward Island to Tabasco, Mexico (Figure 2, 4, & 5) for RFLP analysis in order to determine population structure. Multilocus genetic analysis indicated a similar population structure as that found by Reeb and Avise (1990).

Although these studies indicate an Atlantic/Gulf population structure, other studies have agreed with Buroker's conclusion of a panmictic population. MacDonald et al. (1996) found a lack of genetic structure among six anonymous nuclear DNA loci from oysters in Panacea, FL and Charleston, SC (Figure 3, 4, & 5). These results could be considered questionable as only two populations were used and several markers exhibited deviation from Hardy-Weinberg equilibrium. In 1998, Hare and Avise looked at oysters from Massachusetts to Louisiana (Figure 3, 4, & 5) and found no population structure at three nuclear loci (CV-23, CV-myc, and CV-32 (also used by and Karl and Avise, 1992)). Heterozygotes were identified by Single-Strand Conformational Polymorphism (SSCP) and subsequently sequenced and analyzed. Although Hare and Avise (1998) and Karl and Avise (1992) used the same locus (CV-32) and similar sampling locations, the two studies came to different conclusions by different techniques. On the other hand, Hare and Avise (1996) used a modified version of CV-32 (CV-32.4) and came to a similar conclusion as Karl and Avise (1992) of two separate Atlantic and Gulf populations.

At this time the available genetic data on *Crassostrea virginica* indicate the existence of separate Atlantic and Gulf populations with a transition zone along the eastern coast of Florida (see Table 1). Although scientists have stopped short of defining these populations as subspecies in the published literature, the data suggest that *C. virginica* may be in the process of incipient speciation between Atlantic and Gulf populations.

Crassostrea virginica is not the only western Atlantic species with a notable genetic transition from the temperate Atlantic to subtropical Gulf regions. Similar genetic patterns of population subdivision between Atlantic and Gulf populations can be found in a wide variety of coastal and marine species (Avise 1992; 2000). Some examples are listed in Table 2.

Table 1. Examples of species exhibiting population genetic structure between Atlantic and Gulf populations.

Species	Type	Reference
Atlantic croaker	Finfish	Lankford et al. 1999
Red drum	Finfish	Seyoum et al. 1999
Hermit crab	Crustacean	Young et al. 2002
Southern flounder	Finfish	Blandon et al. 2001
King mackerel	Finfish	Gold et al. 1997
Snapping shrimp	Crustacean	McClure and Greenbaum 1999
Tilefish	Finfish	Katz et al. 1983
Black sea bass	Finfish	Bowen and Avise 1990
Toadfish	Finfish	Avise et al. 1987
Horseshoe crab	Crustacean	Saunders et al. 1986
Seaside sparrow	Bird	Avise and Nelson 1989

Table 2. Genetic studies of population structure in Gulf and Atlantic populations of *Crassostrea virginica.*

Reference	**Genetic Marker**	**Population Structure**	**Comments**
Buroker 1983	allozymes (32 loci)	None	Allozymes can mask underlying genetic variability, and are often subject to natural selection.
Reeb & Avise 1990	mtDNA RFLP	Atlantic-Gulf	Transition zone near West Palm Beach, FL.
Karl & Avise 1992	scnDNA RFLP	Atlantic-Gulf	Transition zone near Stuart, FL.
Cunningham & Collins 1994	reanalysis of Buroker (1983) allozyme data	Atlantic/Florida-Gulf	
McDonald et al. 1996	nDNA RFLP (6 anonymous loci)	None	Deviations from H-W equilibrium. Only 2 sample sites.
Wakefield & Gaffney 1996	mtDNA DGGE and direct sequencing (16s ribosomal locus)	3 haplotypes: Gulf, South Atlantic, North Atlantic	
Hare & Avise 1996	mtDNA RSP scnDNA RSP	Pronounced genetic transition zone along eastern coast of FL.	Major change in both nuclear and mitochondrial allele frequencies around Cape Canaveral, FL.
Small & Chapman 1997	mtDNA RFLP (16s ribosomal locus)	None	Possible slower rate of evolution at 16s mtDNA locus. Only 3 sample sites.
Hare & Avise 1998	nDNA SSCP and direct sequencing (3 loci)	Populations not reciprocally monophyletic between Atlantic and Gulf	
Milbury et al. 2004	mtDNA SNP (16s ribosomal locus)	Discerned transplanted Gulf oysters vs. local Chesapeake Bay oysters	
Hoover & Gaffney 2005	nDNA RFLP (4 non-anonymous loci)	Atlantic-Gulf	Transition zones in eastern and northwest FL.

Laguna Madre Population

A genetically distinct population was found in the Laguna Madre area of Texas by different studies that have included samples from this general area. Groue and Lester (1982) looked at genetic and morphological variation among Eastern oysters in the Gulf of Mexico (Biloxi Bay, Mississippi; West Bay, Texas (near Galveston); Drum Bay, Texas; Aransas Bay, Texas (near Corpus Christi); lower Laguna Madre, Texas) (Figure 5) and found allozyme frequency differences between the lower Laguna Madre and the rest of the sampling sites at the *PGI*, *4MU*, and *GOT* loci. The morphological data, on the other hand, found Laguna Madre and Aransas Bay to be similar while all other combinations of sampling sites to be significantly different when comparing height, length, weight, and length/height index. Morphological variation was believed to be due to environmental influences rather than genetic influences.

In 1983 Buroker found significantly different allele frequencies at several allozyme loci (*Lap-2, Mdh-1,* and *Pgi*) between populations at Brownsville and Corpus Christi, TX. Hedgecock and Okazaki (1984) also found a significant difference in allele frequencies at several allozyme loci (*Lap-1, Lap-2, Mdh-1, Pgi, Tpi, Xdh,* and complete divergence at *Aat-2*) between samples from Campeche, Mexico and Turkey Bayou, FL (near Panacea, FL) (Figure 4&5). King et al. (1994) looked at 16 enzyme systems and two structural proteins in nine oyster populations along the Gulf coast of Texas from East Matagorda Bay to South Bay (Figure 5) and found the Laguna Madre area to be genetically distinct. An intermediate zone was also found between reefs in Northern Corpus Christi Bay and the Upper Laguna Madre (an area of 26 km). Genetic differentiation of the Laguna Madre eastern oyster population may be due to adaptation to hypersaline conditions (up to 35 ppt) created by low levels of precipitation and lack of river inflow as well as selection or genetic drift due to isolation from oyster populations further north (King et al. 1994).

Physiological or Morphological Evidence of *C. virginica* Subspecies

Species and subspecies are often recognized by morphological differences between populations. Due to extreme morphological plasticity, *Crassostrea virginica* has not yet been examined with the goal of identifying such differences. Although in 1951, Loosanoff and Nomejko recognized the existence of physiological races along the latitudinal range of *C.* virginica. Since that time most physiological differences have been found to be related to differences in environmental conditions. Whether additional physiological or morphological studies would be informative is questionable, as any differences between Gulf and Atlantic populations are more likely to be due to local environmental conditions rather than genetic differences (Gaffney 1996).

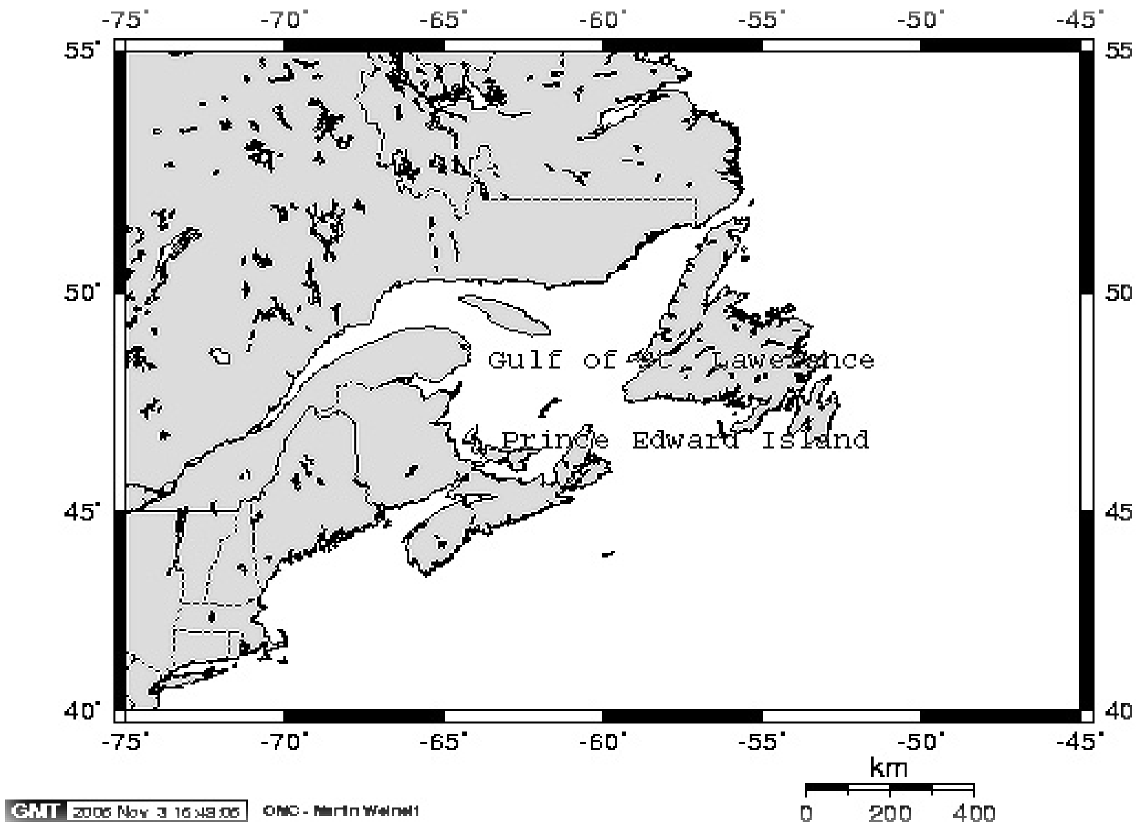

Figure 2. Sampling sites in Canada: Gulf of St. Lawrence (Reeb & Avise 1990), Prince Edward Island (Hoover & Gaffney 2005).

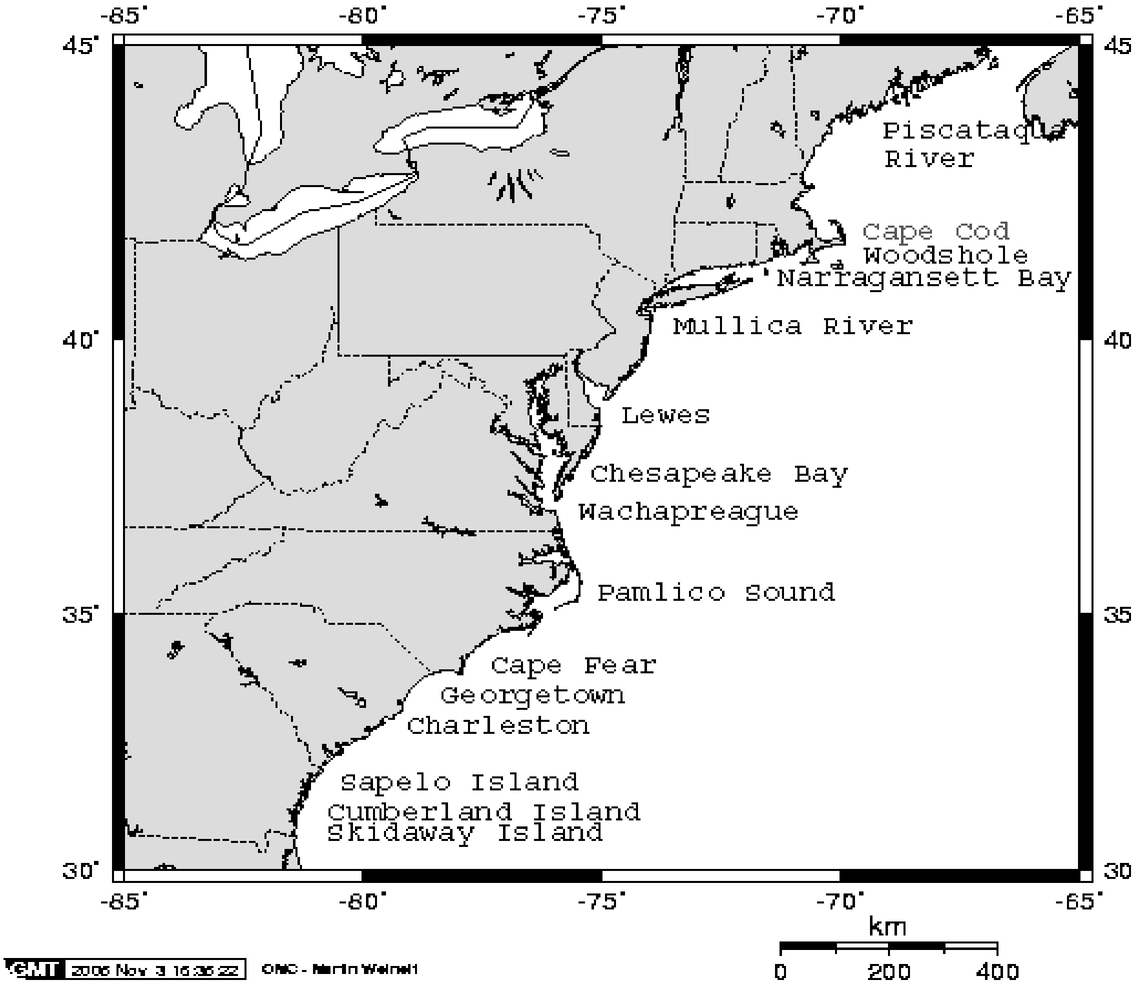

Figure 3. Sampling sites along the Atlantic Coast: Piscataqua River, MA (Hoover & Gaffney 2005), Cape Cod, MA (Buroker 1983), Woods Hole, MA (Karl & Avise 1992; Hare & Avise 1996; Hare and Avise 1998), Narragansett Bay, RI (Reeb & Avise 1990), Mullica River, NJ (Hoover & Gaffney 2005), Lewes, DE (Hoover & Gaffney 2005), Chesapeake Bay (Small & Chapman 1997; Milbury et al. 2004), Wachapreague, VA (Hoover & Gaffney 2005), Pamlico Sound, NC (Small & Chapman 1997), Cape Fear, NC (Hoover & Gaffney 2005), Georgetown, SC (Hoover & Gaffney 2005), Charleston, SC (Karl & Avise 1992; MacDonald et al. 1996; Hare & Avise 1998), Sapelo Island, GA (Reeb & Avise 1990), Cumberland Island, GA (Karl & Avise 1992; Hare & Avise 1996), Skidway Island, GA (Reeb & Avise 1996).

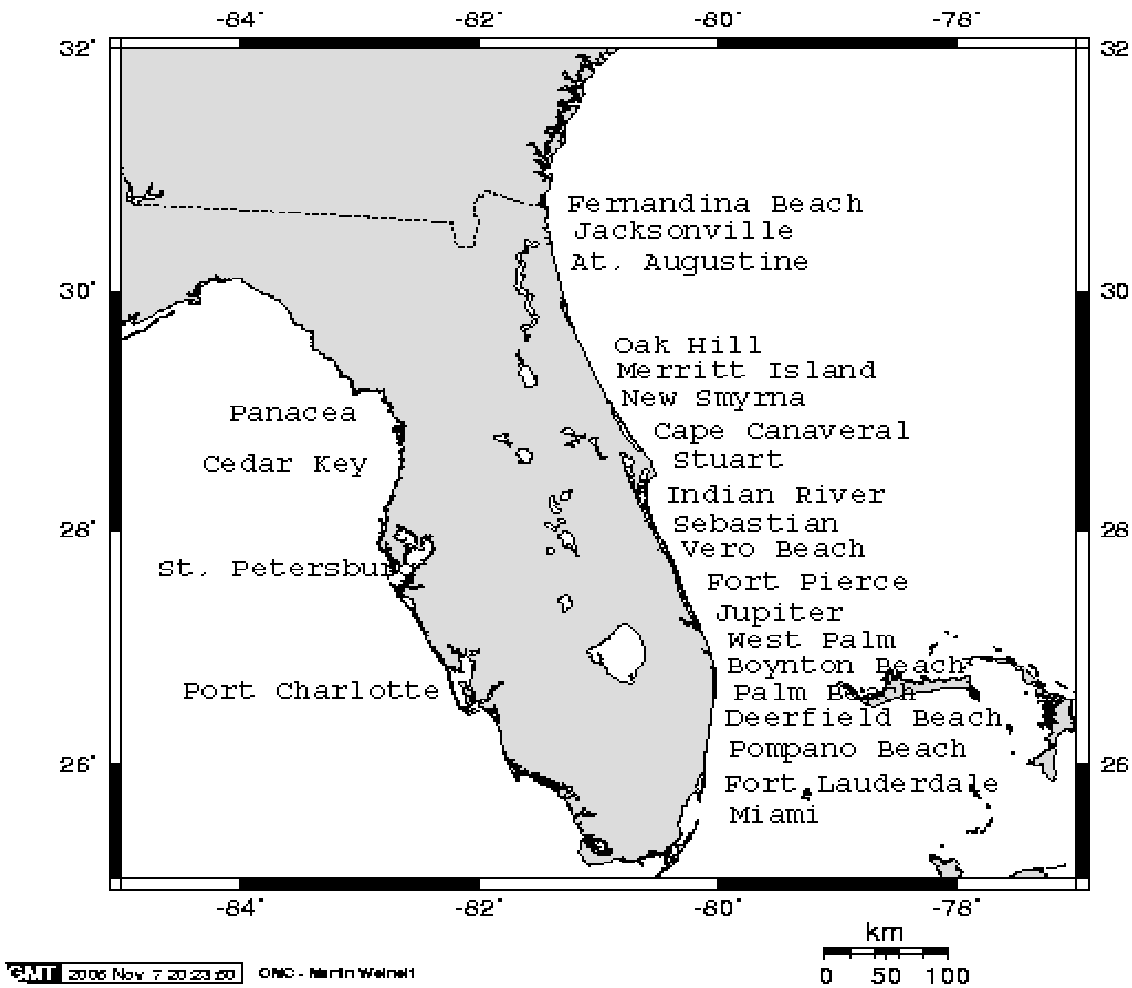

Figure 4. Sampling sites in Florida: Fernandina (Hoover & Gaffney 2005), Jacksonville (Reeb & Avise 1990), St. Augustine (Hare & Avise 1996), Oak Hill (Hare & Avise 1996), Merritt Island (Hare & Avise 1996), New Smyrna (Karl & Avise 1992; Hare & Avise 1996), Cape Canaveral (Buroker 1983), Stuart (Karl & Avise 1992), Indian River (Hoover & Gaffney 2005), Sebastian (Hare & Avise 1996), Vero Beach (Hare & Avise 1996), Fort Pierce (Hare & Avise 1996), Jupiter (Hare & Avise 1996), West Palm Beach (Reeb & Avise 1990), Boynton Beach (Hare & Avise 1996), Palm Beach (Hare & Avise 1996), Deerfield Beach (Hare & Avise 1996), Pompano Beach (Hare & Avise 1996), Miami (Hare & Avise 1996), Cedar Key (Hoover & Gaffney 2005), Panacea (Hedgecock & Okazaki 1984; Karl & Avise 1992; MacDonald et al. 1996; Hare & Avise 1998), St. Petersburg (Reeb & Avise 1990), Port Charlotte (Karl & Avise 1992).

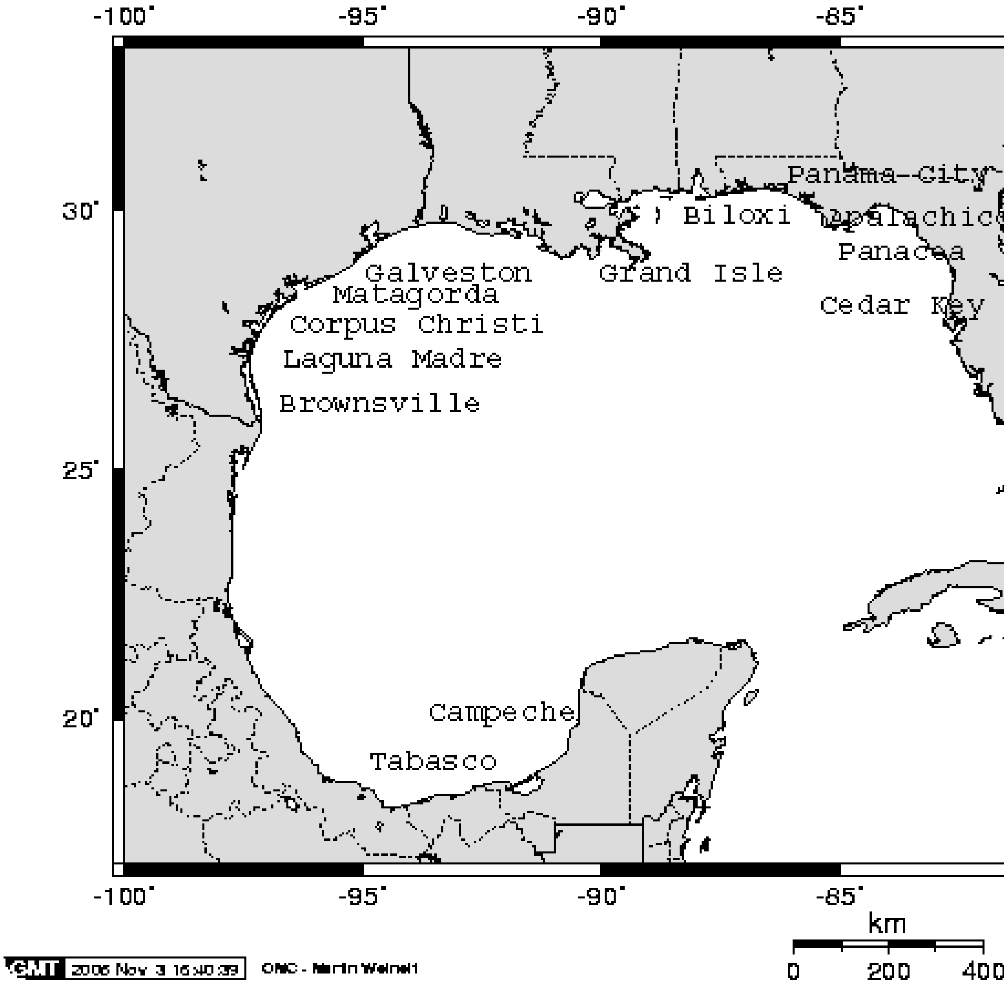

Figure 5. Sampling sites in the Gulf of Mexico: Cedar Key, FL (Hoover & Gaffney 2005), Panacea, FL (MacDonald et al. 1996), Apalachicola, FL (Hoover & Gaffney 2005), Panama City, FL (Reeb & Avise 1990), Biloxi, MS (Groue & Lester 1982), Grand Isle, LA (Reeb & Avise 1990; Karl & Avise 1992; Hare & Avise 1996; Hare & Avise 1996, 1998; Hoover & Gaffney 2005), Galveston, TX (Small & Chapman 1997), Matagorda, TX (Hedgecock & Okazaki 1984; King et al. 1994), Corpus Christi, TX (Buroker 1983), Laguna Madre, TX (Groue & Lester 1982; Hedgecock & Okazaki 1984; King et al. 1994), Brownsville, TX (Buroker 1983; Reeb & Avise 1990), Tabasco, MX (Hoover & Gaffney 2005), Campeche, MX (Hedgecock & Okazaki 1984).

4 Analysis of the ESA's Five Factors

4.1 Habitat Threats

Habitat degradation/loss

Most environmental or habitat alteration problems affecting fishery resources and their habitats are related to socio-economic issues, including many situations that are sometimes classified as "natural", and inadequate managerial attention to these issues in certain areas, or regionally, may be considered an overriding threat to oyster and estuarine health. It is interesting that many early students of the eastern oyster had little to say about the habitat of oysters and its management, although they discussed environmental factors affecting the species (Galtsoff 1964; Coen et al. 1999).

The majority of the contaminant or habitat degradation effects noted below are usually localized and may not affect regional oyster metapopulations, except perhaps in some major urbanized estuaries. Cumulative impacts of several stressors on oysters are difficult to assess, not only at the metapopulation level, but also at local population levels because of variability in spawning success and planktonic larvae dispersal patterns, and temporal and spatial variability of some of the threats. Many or most of these threats, where recognized as more than *de minimus*, are currently under some management effort, but many threats listed below are interrelated with other threats (Mann 2000).

Below is a list and brief summary of most known causes of oyster habitat degradation or loss, not in any priority order:

Fishery-caused

Source factors-

Past unwise harvesting and use practices on public and leased beds, including neglect (Rothschild et al. 1994; Hargis and Haven 1999; MacKenzie 1996; Dugas et al. 1997; Lenihan and Peterson 1998).

Effects-

-Early oyster dredging in some areas reduced the vertical reef structure and later culture methods kept the beds low to facilitate efficient harvesting- this reduced some of the ecological benefits of the reef structure to the oyster and associated species (Rothschild et al. 1994; Hargis and Haven 1999).

-Non-replacement of shucked-shell cultch reduced the hard surface and reef structure that benefits sustainable oyster populations (MacKenzie 1996; MacKenzie and Wakida-Kusunoki 1997).

-Loss of a functionally interconnected system of oyster reefs (functional habitat fragmentation) by depleting or transplanting some smaller oyster reefs/beds to enhance others, or to clear navigational hazards for vessels, has weakened or eliminated the interdependence of spawning oyster populations on a system of functionally connected reefs that capitalize upon variable environmental conditions during the spawning season (Eggleston 1999; Whitlatch and Osman 1999). A system of functionally connected reefs can also help control sediment resuspension (Rothschild et al. 1994; Mann 2000), another threat.

-Harvesting natural seed beds without re-shelling reduced the function of these beds (Rothschild et al. 1994).

-Mariculture or fisheries for other species in or near the oyster reefs can compete for habitat space and other critical resources (Burrell 1997), or contribute inhibitory waste products (biological oxygen demand) (Serve et al. 1999).

-Closure of some oyster beds because of contamination can place excessive harvesting pressure upon remaining open beds and the habitat they provide.

Changes in freshwater, nutrients, organic material, silt, toxic substances, etc. runoff inputs

Source factors-

Point and non-point inputs from human activities within watersheds and water bodies degrade water and sediment quality (Galtsoff 1964; Dugas et al. 1997; NRC 2000; Williamson and Morrisey 2000), and inadequate enforcement of total maximum daily loads (TMDLs) by responsible federal and states agencies in certain estuaries that support oyster populations is considered a major threat in these estuaries.

Effects-

-Eutrophication, stimulated by inadequately controlled nutrient inputs, supports excessive phytoplankton biomass blooms, which contribute to the development of hypoxic/anoxic conditions (see next). Excessive eutrophication may have a negative effect in some estuaries, while light to moderate inputs of nutrients may enhance primary and oyster productivity where biological potential is limited (Kirby and Miller 2005).

-Eutrophication can support increased incidences of toxic or harmful algal blooms, “red or brown tides” that kill or inhibit oyster survival or growth at all stages of their life cycle (Loosanoff 1964), and dense inhibitory macro-algae (e.g., sea lettuce, *Ulva*) coverage can smother shallow oyster beds (Galtsoff 1964).

-Eutrophic populations of plankton can increase the abundance of planktivores, such as coelenterates and ctenophores, which can prey upon oyster larvae (MacKenzie 1977).

-Eutrophication can cause changes in phytoplankton community composition, e.g., increase the abundance of species that are too small or large to be effectively filtered and retained (non-toxic picoplankton blooms) and reduce the abundance of taxa most useful as food to oysters (Loosanoff 1964).

-Hypoxia/anoxia has become more common in the deeper parts of many estuaries and is linked to eutrophication (Hagy et al. 2004) (Funderburk et al. 1991; Dugas et al. 1997; Lenihan and Petersen 1998). Even short periods of hypoxia/anoxia can be stressful or lethal to oysters, especially spat or seed, because they will not have the energy reserves to remain closed for too long.

-Waste disposal, including treated and untreated sewage and cooling waters affect the water quality where oyster were or are found and involve eutrophication and toxic chemicals (MacKenzie 1996; Dugas et al. 1997).

-Silt, from a variety of sources including upstream land use (Ulanowicz and Tuttle 1992), can cover and "smother" shell, beds and other oyster-suitable substrate inhibiting oyster abundance (Galtsoff 1964; MacKenzie 1996). This "muck" can also cause a concurrent shift of the benthic community from filter-feeding to deposit-feeding species/mode, which in turn, can contribute to the siltation problem by creating silt retaining beds, i.e., macro-infaunal tube fields, or recycling buried silt to the surface as erodable feces (Serve et al. 1999). Oyster eggs and larvae are most sensitive to suspended sediment (Davis and Hidu 1969).

- A variety of toxic waste inputs (chemicals, oil, etc…) critically affect oyster larvae and later life stage health and survival (Galtsoff 1964; Calabrese et al. 1973; Funderburk et al. 1991; Roesijadi 1996; Capuzzo 1996; Dugas et. al. 1997; MacKenzie and Wakida-Kusunoki 1997; Dauer et al. 2000; Wintermyer and Cooper 2003), including possibly acting as endocrine disruptors (Nice et al. 2003).

-Increases in shellfish bed closures because of human disease risks cause a loss of maintenance attention to beds within those closures, allowing silt to accumulate or destructive alternate uses of the beds to happen, e.g., dredged for shell for non-mariculture purposes (Stiles 1911; MacKenzie 1996, 1997; Dugas et al. 1997).

-Synergistic effects of multiple factors, which are not individually harmful, can become harmful by accumulatively exceeding physiological stress thresholds of some life stages of the oyster (Galtsoff 1964; Shumway 1996).

Coastal development

Source factors-

Increased use of coastal areas for residential, commercial, and recreational purposes (urbanization) alters the character of the land and its watersheds, and affects down-stream or adjacent estuaries that have supported oyster populations. United States coastal counties comprise 17% of land area, but are inhabited by 53% of the population; by the year 2008, the coastal county population is expected to increase by approximately 7 million (Crossett et al. 2004). Urbanization competes with the property fishermen need to oversee, maintain, and use oyster stocks. This issue is almost ubiquitous in all coastal areas, or could be, and its potential multiple effects on oysters and their habitat can vary greatly among areas, even though specific cause and effect relations are poorly documented.

Effects-

- A variety of coastal development factors cause the reduction in submerged aquatic vegetation (SAV) beds and other habitats (wetlands and ecologically serviceable watershed habitats) that may be linked to oyster populations via total ecosystem health considerations.

-Changes in runoff inputs noted above, including more impervious surfaces and storm drains that pour excessive or contaminated waters directly into estuaries, can alter the hydrography and quality of aquatic habitats used by oysters (Burrell 1997; Dugas et al. 1997). There may be a complex relationship between temperature and salinity and their affects on oyster spat set, survival and growth that may reflect genetic or environmental adaptations of parent stock. Subtle changes in the mix of temperature and salinity, even to a long evolved estuarine species, may be important especially if a local stock has adapted to a specific natural cycle.

-Use of dredged or shucked shell stock for land-based construction purposes, e.g., lime, driveways, roadbeds, etc. depletes the supplies of clean cultch that sustain oyster populations (MacKenzie 1997b).

-Loss of shore line vegetated buffer zones, e.g., marsh grass and mangroves, can increase runoff and erosion, as well as bring lawn/garden chemicals in closer direct contact with the estuary and its oysters.

-Increased recreational boating traffic (Burrell 1997) increases turbidity, shoreline erosion, and damages SAV beds as well as creates a demand for the removal or dredging of oyster shoals to reduce navigation hazards (Kelty and Bliven 2003).

-Increased local atmospheric pollution, such as acid rain and associated nitrogen inputs, from coastal development's "air sheds", (e.g. vehicle exhaust, emissions from new pulp mills, or other industries involved in coastal development) can be deposited onto estuarine water bodies (Cooper and Brush 1991; Paerl and Whithall 1999).

-Increased demands on natural resources, such as underground or upstream water supplies, can alter the hydrographic character of the estuary by diminishing freshwater inputs that help control certain predators, parasites, and diseases (Burrell 1997).

-Loss of shoreline forests (MacKenzie 1997b), besides directly altering watershed hydro-geodynamics, can alter wind exposure in smaller estuarine tributaries that can affect the wind-driven component of intertidal and subtidal oyster larvae dispersal processes.

-Because coastal and regional development usually requires increases in electrical power supplies, power generating plants are built that use estuarine waters for cooling. Entrainment of oyster larvae into the cooling waters of power plants in some estuarine areas can reduce larval stock density from local areas and impact spat recruitment. Super heated cooling water may impair un-entrained oyster larvae near the outfall, but some warmer effluent from power plants in northern waters may alternately enhance larval recruitment if they recycle >20ºC, chemically untreated, cooling water back into areas containing spawning oysters, if ambient temperatures are notably below this level during the extended oyster spawning season and phytoplankton food sources are not degraded in the effluent fields.

- In some areas, the recent installation of treated wood pilings, bulkheads, or docks, can introduce metals, such as chromium, copper, and arsenic (CCA), at levels which can be temporarily toxic to oysters (Weis et al. 1995). If this use occurs to support boating, then other toxic metals can also be released from antifouling paints, such as tributyl tin, used on these boats.

Habitat user conflicts

Source factors-

Estuaries are increasingly being used by people. This has put the maintenance or restoration of oyster reefs or beds in conflict with other existing or proposed uses.

Effects-

- Dredging channels and harbors can increase salinity, tidal amplitude, suspended solids/turbidity, or change currents or flow patterns. Dredged sediments may also be deposited directly on reefs. These changes can adversely affect oysters (MacKenzie 1996; Dugas et al. 1997).

-Channel dredging to accommodate nearshore access to docks on newly developed coastal land also can change the hydrographic characteristics of parts of estuaries. This may influence the settlement density of oyster spat. The use of these new channels by vessels can increase shoreline erosion and also suspended solids burdens (Dugas et al. 1997).

-Navigation of larger vessels, such as tugs and barges in nearshore environments, may impact reefs by covering settlement surfaces with sediment or by direct contact from the vessel hull or propeller.

-Shell mining for non-mariculture purposes depletes potential shell stock for oyster reef/bed sustainability and fossil shell that can be recycled as cultch, and leave large holes on the bottom of estuaries (MacKenzie 1996).

-Freshwater dams and diversions to support coastal and other land development reduces or minimizes natural seasonal variability in fresh water inputs alter the habitat for oysters.

-Construction of breakwaters or other non-porous man-made structures within an estuary or filling in shorelines with roadways, bulkheads and dikes can alter hydro-geophysical processes, e.g., restrict tidal flows, involving salinity and oyster larval distributions, and silt deposition budgets in some areas.

-Agricultural practices, including soil and chemical-application management, still affect some estuaries presently or recently containing oyster populations.

-Deforestation and lumbering in some areas has altered the hydro-geophysical processes within watersheds supplying down-stream estuaries and their oyster populations (MacKenzie 1997b).

-Impacts of other fisheries (e.g., clam dredging, shrimp trawling, etc.) may include the re-suspension and mobilization of silt if these towed gear are used near oyster beds, and if this silt reaches the oyster beds, it can be excessive and damaging to the persistence of the oyster populations on those beds (Dugas et al. 1997).

Natural environmental factors

Source factors-

This involves any number of natural environmental, biological and climatic factors that are primarily beyond the control of man, but when they interact with oyster populations on an event- or gradual trend-basis can influence habitat suitability for oysters, at least temporarily, (e.g., climatic change or variation, severe weather events, change in competitive species distributions).

Effects-

-Increases in temperature, e.g., via global warming, can change the distributions of oysters, their predators, competitors and associated diseases especially at extreme distribution or tolerance limits (See Section 4.3).

-Climate change, most likely, will affect all coastal ecosystems in the future. Oyster populations are, therefore, expected to be subject to fluctuations and perturbations as a result of climate change and sea level rise.

-Changes in the distribution of competitive species (non-exotics), often associated with changes in environmental conditions, or reflecting natural pulses of high abundance of the competing species for unknown reasons can negatively affect oyster reefs/beds (MacKenzie 1981; White and Wilson 1996), e.g., the hooked mussel, *Ischadium recurvum*.

- Unintentional introductions of exotic species can alter or compete for the same or similar suitable habitat {e.g., smothering tunicates (e.g., *Didemnum* sp.)} or other ecological resources; or they may act as predators, (e.g., veined rapa whelk, *Rapana venosa*) (Mann and Hardy 2003). This may be a greater problem in the future, if introductions of alien estuarine species into areas where the oyster occur continue at the present or accelerated rate.

-Severe weather events, such as hurricanes, can cover oyster beds with silt, wash oysters off beds, or impose extended “freshettes” on oyster beds to the degree that they are significantly impaired and need restoration (Berrigan 1988, Dugas et al. 1997; Perret et al. 1999;) or they become un-economical to restore and are abandoned, e.g. Narragansett Bay RI (MacKenzie 1996, 1997a) (See Section 4.5).

-The natural filling and closure of some lagoon inlets, often after a major storm, if not reopened can cause lagoons to become hyper/hypo-saline for oysters depending upon the dynamics of freshwater inputs to the lagoon (Dugas et al. 1997; MacKenzie and Wakida-Kusunoki 1997).

-Land subsidence, especially along the northern Gulf of Mexico coast, and associated coastal erosion can alter habitat suitable for oysters.

Coastal demographics/social changes

A developing and perhaps over-riding threat to oyster populations and their habitat which overlaps several or perhaps all ESA factors is the impact of the destabilization of local fishery dependent communities because of gradually or opportunistically changing demographics and competition for the resources that these communities depend upon. Dyer and Leard (1994) discuss how stable oyster fishery communities in Florida and Louisiana have sustained oyster populations and productivity at less annual variance and greater productivity through a community ownership concept. They did so better than other Gulf States, who do not have this same relationship. The relationship of a coastal community to its oyster resources can be extremely important to the sustainability of at least local oyster populations.

Many communities that rely upon the harvesting of oysters (and other seafood) have developed a "folk management" approach based upon decades of trial and error experience passed down through generations. They have often developed a useful relationship with regulatory agencies, as well. This experience combined with a sense of local community ownership of the resources, including leasing, has done well to sustain oyster populations and fisheries for well over a century in Florida and Louisiana. More variable and less productive oyster fisheries exist in other states without this strong generational community association, according to Dyer and Leard (1994).

At present, there may be new, developing demographic and sociological forces that threaten these oyster stewardship communities that can break down the generational continuity in participating in the labor intensive and fiscally limited fishery. These forces can be competing for resources on land and in the water that these communities (and the sustained oyster populations and the habitat they create and support) may depend upon. These forces can be enhanced in response to a catastrophic event(s), such as severe hurricane damage, or to gradual shifts in social demographics and in the value of the shore to a different demographic group.

In the past, local oyster dependent communities were able to endure occasional hurricane damage as part of the environmental variability they had to accept, in the same way farmers accept/adapt to weather. However, today there may be less acceptance of this situation as there are other alternate and/or rewarding employment opportunities for people in or outside of these communities. Many may not want to continue to invest in the fishery or the fishery dependent community after suffering severe damage. The decline of a generational investment in oystering and the resource can lead to loss of productive oyster beds and leased grounds maintenance and less interest in the long-term sustainability of the fishery. Thus, the oyster populations and habitat can suffer as the coastal community gradually turns away from its traditional fishery dependence. This may result in resources that support the fishery (e.g., shoreline land and dockage) being converted to non-fishery uses such as residential or commercial development. This development can exacerbate coastal environmental problems or threats, such as changes in water flow and increases in siltation and pollution, which are considered threats to oysters (as discussed above).

This change in coastal use can also be accelerated by the current retirement trend in the "boomer" generation who are relatively wealthy and are moving to warmer climates and cheaper cost-of-living areas, such as in many areas of the south. Many such retirees seek water front property and places for their recreational boats, and perhaps better navigation channels for these vessels. Storm-damaged fishery communities that are losing generational participation can be vulnerable to being sold in tempting real estate deals that reduce the infrastructure needed to sustain managed oyster fisheries.

Many local oyster fishery communities will be faced with the issue of continuing to support their heritage fisheries and the type of community that developed around these fisheries. Also, there is the potential they will have to accept higher tax rates due to the increase in expensive water front residences and expanded service businesses that will follow this influx of outsider home owners. This can also result in community stress and destabilization as well as a shift in the political attention given to traditional oyster fisheries and the environmental conditions they require. Although the oyster population in many areas will survive this change, they may be weakened or extirpated in local situations, if stewardship declines and environmental protections are not adequate.

This demographic/social change threat to oysters may be presently greatest in the Gulf, but it has occurred and continues in the south and mid-Atlantic regions, as well.

Many of the habitat threats listed above have likely abated to some degree in many areas, except perhaps those of coastal development, through environmental management efforts. The effects of some threats may be immeasurable. These threats, combined with the natural variability in oyster recruitment in many estuaries, will make it difficult or impossible to attribute specific cause and effect relationships of any current diminished oyster distributions with the many threats or stressors man has induced, except in controlled experimental situations.

4.2 Overutilization for Commercial, Recreational, Scientific or Educational Purposes

Overview of Harvest

Eastern oysters have been harvested as a food source and their shells have been used as construction materials and agricultural products for thousands of years. Warnings that segments of the Atlantic coast oyster resource were being over utilized or overfished began early during the peak oyster producing years and extended through the 20^{th} century (Winslow 1885, 1889; Brooks 1891; Stevenson 1894; Haven et al. 1978; Hargis and Haven 1988). Observation of commercial catches provided the primary information on which the overfishing predictions were based and included reduction in size class composition, catch per unit effort (CPUE) decreases, and spawning stock biomass concerns raised due to local depletion of stocks by intensive harvest and later by reduced spatfall (Hargis and Haven 1995). Other authors have shown that excessive harvest of oysters on the Atlantic coast followed a pattern that began near northeast population centers and moved progressively down the coast. As oyster landings diminished in one area, oyster fishermen moved southerly to the next oyster area harvesting with more efficient gear than locals, taking seed to replenish stocks in their home areas, and allowing local fishermen to learn harvest techniques with the new gear. Landing declines continued despite later attempts to regulate the harvest (Figure 6) (Kirby 2004; Hargis and Haven 1995; Chestnut 1951). Recent investigations in Delaware Bay and the Maryland portion of Chesapeake Bay indicate the primary cause of more recent (mid 1990s) declines in oyster abundance was parasite-based mortality (Fegley et al. 1996; Homer et al. 1996).

Consumer demand fueled the efforts to maximize early oyster harvests. Oyster canning technology and railroad development during the mid 1800s opened markets for eastern oysters as far west as St. Louis and the increased harvests reduced oyster prices lower than those for beef, poultry, and fish (MacKenzie 1996). Oysters became a regular part of the American diet during oyster season. New Yorkers averaged two meals of oysters per week and consumed 500,000 bushels of oyster per season in the early 1900s. The people of New Orleans consumed 750,000 bushels of oysters per year during the same time period (MacKenzie 1996). Establishments specializing in serving oysters such as cellars, saloons, parlors, bars and lunchrooms were common (Ingersoll 1881). Lipton and Kirkley (1994) found that demand for oysters dramatically declined during 1984-1994 as a result of health/nutrition, product safety, water pollution, and adulterated product concerns. The apparent decline in demand for oysters occurred while seafood consumption in general became an increasingly important part of the American diet as a trend toward more healthful eating habits (Lipton and Kirkley 1994).

Oysters are primarily harvested for their meats but shells left over after shucking and empty shells taken as bycatch in fishing operations were used historically for landfill, road building, construction, lime production, and poultry grit (Hargis and Haven 1999). The U.S. Departments of Commerce and Interior gathered statistics on production of oyster shell byproducts until 1945 (Hargis and Haven 1999). Since the primary oyster habitat is composed of natural oyster shell deposits, harvesting affects not only existing oyster populations but also critical oyster habitat because of the removal of shells. In fact, the health of the oyster resource is so closely linked to the habitat created by the deposition of their shells that many investigators have used the condition of this shell habitat as an indicator of oyster population health (Haven and Whitcomb 1983; Rothschild et al. 1994; McCormick-Ray 1998; Lenihan and Peterson 1998). Several reports cite the loss of oyster habitat due to fishing and coastal development activities as an important factor in the decline of oyster populations (Berrigan et al. 1991; Rothschild et al. 1994; Hargis and Haven 1999; NCDENR 2001). The use of oyster shell for purposes other than reef restoration has been well documented; however, measures to regulate those uses have not. Most states now have cull-in-place regulations and programs to purchase and replace oyster shells harvested on public bottoms. Provisions to ensure use of oyster shell for habitat, such as banning their use in septic fields and disposal in landfills, are often obscure local ordinances. Oyster shell is still widely used in landscaping and in dietary supplements.

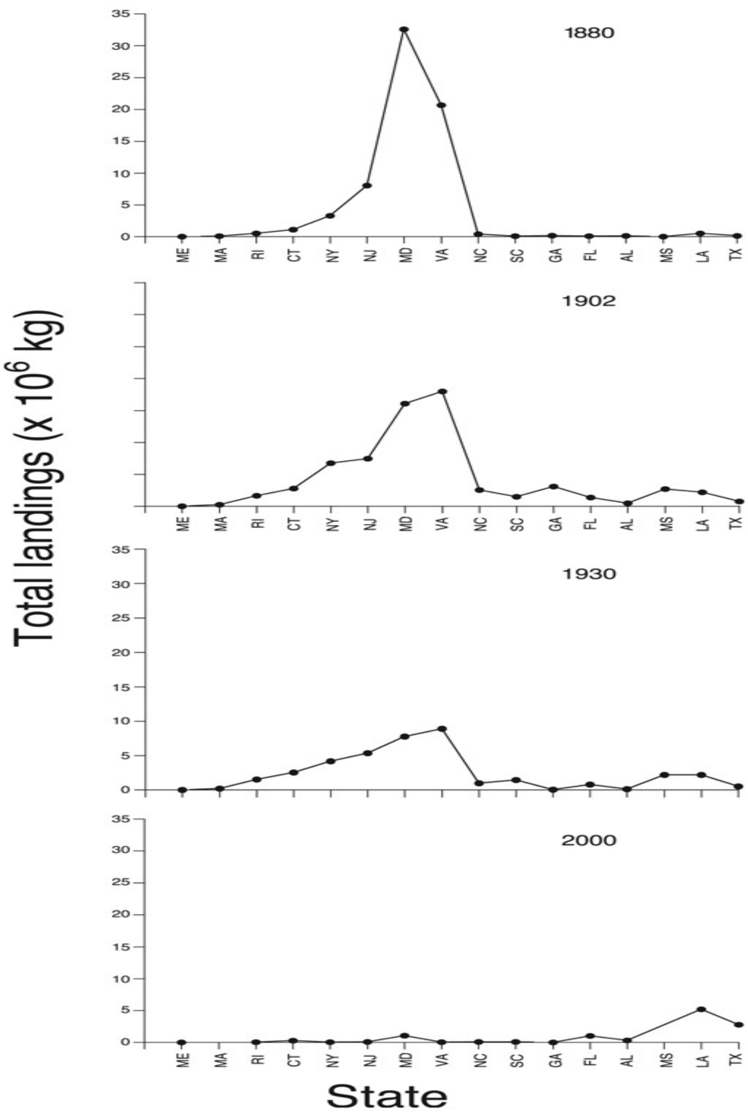

Figure 6. Landings of *C. virginica* that show a linear sequence of fishery expansion and decline along eastern North America between Maine and Texas (from Kirby 2004).

Commercial Utilization by Region

Traditional assessments of oyster resources rely almost exclusively on information from fisheries dependent data. Use of landings data to assess abundance is confounded by the quality of reporting, various reporting mechanisms, landings and dockside values, and commercial markets.

Fisheries independent data are obtained through surveys designed to directly assess the status of a population, independent of the fishery.

Unless otherwise noted, the information presented in this section is summarized in MacKenzie 1997b. The discussion below focuses on the use of dredges in the fishery, the importation of seed oysters, cultch planting activities and other management measures as indicators that the market demand for oysters exceeded the ability of the resource to produce them, or overutilization. Other mitigating factors such as substantial impacts due to disease, storms and market conditions are also included. Oyster abundance assessments were used if available. Unless otherwise noted, the information presented in this section is summarized from NOAA Technical Report NMFS 127: The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe by MacKenzie et al. (1997).

Northeast – Maine through Long Island Sound
This was the first area to be heavily exploited for its oyster resources. By the late 1700s oyster catches were declining and states passed laws limiting harvest. Dredges were introduced in some areas in the early 1800s, and catches declined even more rapidly despite strong demand. Seed oysters importation began around 1820 and industry production peaked in the early 1900s. Oyster production was limited due to low demand after peak landings in 1910 until 1938 and again from 1988 to 1996. Oyster production was impacted by major hurricanes in 1938 and 1950 that covered many beds with sediment and destroyed harvest vessels. From around 1950 to the mid-1980s, inadequate supplies limited oyster production (MacKenzie 1997b). The majority of the oysters in the region currently are produced in Connecticut. Production there was greatly increased by massive private and government cultch plantings during 1988-1991 (MacKenzie 1997b). However, NMFS landings data indicate that production has declined steadily since 1999.

Maine – The Damariscotta River beds were destroyed by coastal land development and wild oyster harvest ended there around 1840; however, small oyster beds were present in several locations along the rest of the coast into the 1960s. Primary production of eastern oysters in Maine is through aquaculture. Wild oysters harvested from the Piscataqua River are depurated before reaching markets (Wallace 1997).

Massachusetts - Native oysters were considered depleted by the early 1800s in Massachusetts. Leaseholders began importing seed shortly thereafter. In the early 1900s Connecticut growers obtained leases in Wellfleet Harbor to grow out seed from Long Island Sound. The industry declined after the hurricane of 1938. Subsequent oyster production in Massachusetts waters, mainly from aquaculture, is difficult to summarize because management and reporting are at the municipal level.

Rhode Island - Attempts to develop the oyster industry in Narragansett Bay began in 1822 with the initiation of a bottom lease program. Seed oysters were imported from Chesapeake and Great South bays and resulted in landings of 660,000 bushels by 1878. After 1880, Connecticut growers took over oystering in Narragansett Bay as they did in Wellfleet Harbor. The 1938 hurricane and a lack of seed from Connecticut caused a sharp decline in landings. Few oysters were planted or harvested from 1960 until 1996 when spat sets on public beds planted with cultch material in 1993/94 began to produce (MacKenzie 1997b). Oyster landings rose to about 45,000 bushels in 1997 then slowly declined to an average of around 7,500 bushels for the period of 2001-2004 (NMFS Landings Data).

Connecticut - Connecticut has the most intensive oyster farming operations in the region. A large public seedbed of about 3000 acres supplied seed oyster needs in the early years and continued to produce until around 1945. Importation of seed oysters began in the 1830s and reached 750,000 bushels in the 1850s. Leaseholders began planting shells on their bottomland to increase local seed supplies around 1900 and planted up to 3 million bushels of shells per year. New sanitation laws caused declines in demand and prices around 1906. The 1938 hurricane destroyed many beds as well as another storm in 1950. Starfish, drills and sedimentation destroyed most seed until the 1970s when new harvesting and predator control methods were developed. Production further increased when the State and Tallmadge Brothers Oyster Company vastly increased cultch planting on the seedbeds. Millions of bushels of shells were planted from 1987 through 1991. Seed production and landings responded until 1997 when the parasites *Haplosporidium nelsoni* (MSX) and *Perkinsus marinus* (DERMO) became active (MacKenzie 1997b).

New York - Great South Bay was the major oyster producing area in New York until the 1938 storm. Oyster growing operations involved transplanting natural seed from low salinity sites in the eastern sound to western high salinity areas. After 1870, the local seed supply was supplemented by imports from Connecticut. Poor market demand plagued the fishery from 1910 until 1938. The 1938 storm opened inlets, which increased salinity levels throughout the bay, allowing oyster drills to destroy all the seed. Few seed were planted during the 1940s and 1950s. Around 1960, MSX became active in the bay and little planting or harvesting was done until hatchery production began about ten years later. During the 1980s and 1990s, about 90% of New York's oyster production came from hatchery-reared seed. Some wild harvest production was reported in the early 1990s (MacKenzie 1997b). There was an oyster fishery in the Hudson River estuary from the 1600s to the 1800s with seed still being harvested in the 1950s (Pers. Comm. Steimle 2005).

Raritan and Barnegat Bays

Growers planting seed produced most of the oysters in Raritan Bay. Seed was available from local sources until demand caused seed to be imported from Chesapeake Bay beginning around 1820. In 1915, pollution began to curtail harvests when western Raritan Bay was closed. Other areas were closed in the 1920s and by 1930 oyster harvesting ceased in the area (MacKenzie 1997b).

In 1880, the seed oyster beds of Barnegat Bay were already suffering from over harvesting. Seedbeds in other nearby areas were also being depleted by 1892. Further overharvesting and increased salinity caused by changes in Beach Haven Inlet during a major 1919 storm continued to reduce the fishery. Additional increased salinity and the resultant increase in predation occurred in 1925 when the opening of Point Pleasant Canal introduced salt water into the head of the bay. Landings in the bay have been insignificant since 1950. A small fishery has existed in Great Bay since around 1950; however, MSX and *P. marinus* mortality caused most growers to leave the fishery (Ford 1997) (See Section 4.3).

Delaware Bay

The early Delaware Bay oyster fishery was conducted using tongs and the oysters were taken for direct marketing or shipped to Connecticut and Massachusetts as seed for growout. During the 1800s, dredging was introduced to the bay to meet increasing demands for out-of-state seed. By 1843 written descriptions already existed of dredges dragging shells from the tops of reefs and increasing the size of beds by scattering the shells. At the time these circumstances were thought to be good for the seedbeds.

Overharvesting of seedbeds and predation caused some areas to cease production by1900. A law to protect the seed beds required that seed be harvested by sail powered vessels only. This requirement was removed during WWII, increasing deterioration of the seedbeds. Unexplained seed oyster mortalities in the 1940s and 1950 put the beds at an all time low. Delaware River flow was examined and revealed low flow allowed oyster drills to move upriver in high salinity to the seedbeds. Higher river flow returned in 1968 as did seed supplies and in 1972 a tremendous set restored seedbeds that had not produced for 50 years. This set and others over the next 12 years sustained the industry through 1985. MSX mortalities began in 1957 and continued through the early 1970s. Modified growout strategies and better care of the seed beds allowed a modest recovery until 1985. MSX returned in 1985 and caused closure of the seed beds until 1990. *P. marinus* related mortality also became a problem in 1990. The seedbeds were closed 6 years between 1987 and 1997 due to disease and poor recruitment. Seed beds returned to production twice after serious depletion, 1972 and 1990-91 (Ford 1997). However, as noted above, seed supplies are currently low due to five years of poor recruitment and as a result, oyster harvest in the bay is severely restricted.

Laws allowing leasing of bottoms for oyster growout were enacted in 1856 in New Jersey and 1873 in Delaware. Shell was returned to the seedbeds for several years beginning around 1900. Good sets resulted and leased acreage increased from 12,000 acres in 1900 to 30,000 acres in 1914. From 1880-1930, Delaware Bay harvested 1-2 million bushels annually. From 1930-1957 landings declined to 1 million bushels per year. Failure to return shells to the beds, drought induced drill predation, the Depression and shellfish sanitation concerns were cited as possible reasons for the decline (Ford 1997).

An 1875 law required all oyster shell caught during harvest to be landed and deposited for road repair. Continual removal of cultch material over the next 25 years hastened the deterioration of public beds; a condition stressed in all reports of the period. New Jersey officials purchased shell and returned it to the seedbeds for several years beginning around 1900. Legislation requiring seed planters to return 60% of the shell from all oysters harvested was passed in 1946 but was repealed by 1979. The state planted small amounts of shell afterwards.

Chesapeake Bay seed were imported at least since 1829 because Delaware Bay seed could not meet the market demand. Seed shipments were stopped around 1900 because Virginia officials were alarmed at the drain on their resource. In 1950, seed imports restarted but were stopped in 1957 to stop the spread of MSX.

Chesapeake Bay

Huge amounts of seed oysters were transported from Chesapeake Bay to northern states for direct sale and planting during most of the 1800s. In 1879, 2.18 million bushels were used for this purpose (Ingersoll 1881). After tremendous oyster landings between 1870 and 1895 of up to 20 million bushels per year, landings dropped steadily until the1930s. The declining landings over 35 years probably indicate declining supply. The excessive harvest removed surface shells from oyster reefs developed over centuries, reducing recruitment. Other thin-based beds were potentially totally removed. Market conditions (including concerns for shellfish safety) also contributed to reduced landings later in the period. Production from1930 to 1955 was relatively consistent as management practices and shucking house shell plantings were adequate. Production fell again in the Fifties and did not recover in Virginia (MacKenzie 1997b).

Maryland began fossil shell planting in 1960 with 5-6 million bushels planted in lower state waters with histories of good sets. Skip jacks were hired to move seed up the bay after set. Maryland landings rose to more than 2 million bushels during the mid 1960s through the early 1980s. MSX returned to the Maryland portion of the Bay in 1981 along with the invasion of *P. marinus*. Landings subsequently fell to levels of 100,000 to 200,000 bushels per year (MacKenzie 1997b).

Virginia oyster landings fell steadily from 7-8 million bushels per year in the 1880s to the period from 1935 to 1955 when production ranged between 2.5 –3.7 million bushels per year. The main cause of the decline seems to have been a great reduction in the supply of oysters on the public grounds even though hand and patent tongs were the only gear allowed on public beds in deep water areas. The wild populations could not withstand the steady harvest pressure with concurrent siltation, shell fouling and inadequate shell replacement (MacKenzie 1997b). Cultch planting on public grounds began in 1928 with 160,000 bushels. From 1 to 3.5 million bushels were planted per year in the 1960s and 1970s but cultch plantings were made primarily in support of seed oysters for lease production. Virginia leaseholders used shucked shell to improve their planting grounds and also created thousands of acres of suitable oyster habitat.

From 1859 to 1959, more than 200 million bushels of seed were taken from the James River, VA. Transplanting of James River seed oysters by tong fishermen reduced rock height by 1.5 meters (58.5 in) over a 90-year period indicating impact to the habitat. Due to declining harvests in other areas, the James River was used for direct harvest of market oysters following the 1986/87 season and market oystering was concentrated there through the 1990s. The state restricts harvest in the James River to conserve the remaining stock and many fishermen have left the fishery (MacKenzie 1997b). Recent landings for the state have been below 20,000 bushels per year (NMFS data).

Beginning in 1959 MSX killed most oysters greater than 50mm (2 in.) in high salinity (>15ppt) areas in Virginia. During the1980s, annual mortality ranged from 50-70%. MSX was also the likely cause of a huge drop in setting densities since the early 1960s due to reductions in spawning stock (MacKenzie 1997b). A soup oyster fishery utilizing 1.5-2 inch (38-50mm) oysters began in 1957 in the James River. Soup oysters could be marketed directly with no further growout and avoided some of the disease mortality. Also, there was no market for seed due to MSX after 1960. The soup oyster fishery ended in 1976 when Kepone was found in James River.

South Atlantic - North Carolina through the east coast of Florida

North Carolina subtidal oyster landings accounted for most of the south Atlantic harvest until the 1890s when canneries were established in South Carolina and Georgia. South of Pamlico Sound oyster resources are primarily intertidal. *P. marinus* mortality became a significant factor affecting oysters in Pamlico Sound in 1991. It is only a problem in more southern areas during extreme drought conditions. All of the states in the region have summer season harvest closures except Georgia. Oyster production is at an all time low due to pollution closures, lack of markets, disease in subtidal oysters, habitat impacts and labor shortages. Closures to harvesting due to pollution removed 24% of the available harvest area by 1990. Limited relay of polluted oysters to public bottom and leases for depuration is used to reduce the effect of the closures (Burrell 1997).

North Carolina - The North Carolina oyster resource was not fully exploited until 1889 when fishermen from northern states began harvesting in Pamlico Sound with dredges and mechanical tongs (Chestnut 1951). The state attempted to reduce the effects of dredging by limiting the area where the gear could be used in 1897. However, as catches declined the area open for dredging increased. Oyster landings peaked in 1902 and seed oysters from North Carolina were also being shipped to Chesapeake and Delaware bays during this time period (Chestnut 1951). Since 1955 dredging area has decreased (NCDENR 2001). Cultch planting to increase oyster harvests began about 1915 in North Carolina but consistent operation of the program was not achieved until 1947 (Marshall et al. 1999). A dredge weight limit was also enacted in 1947 along with a daily catch limit. Oyster landings continued a general decline and fell below 200,000 bushels per year in 1962. Catches were averaging just over 100,000 bushels per year in 1989 when the state began to experience mortality from *P. marinus* infections brought on by a severe drought (NCDENR 2001). Landings fell to around 40,000 bushels per year in 1993 and have not recovered. Since 1993 more than 95% of North Carolina's oyster landings have come from intertidal beds in the southern part of the state (NCDENR 2001). Harvest from these intertidal oyster resources has remained steady in part due to the greater setting intensity and faster growth of these stocks. CPUE data is monitored to assess sustainability of the stocks. The oyster season has closed early in recent years due to low supplies of harvestable oysters (NCDENR 2001).

South Carolina - South Carolina's oyster landings are generally higher than those in North Carolina but they have declined similarly. Factors causing the decline are believed to be impacts from industrial and residential development, channelization and waterway construction, poor markets for intertidal oysters, labor shortages and pollution closures (Maggioni and Burrell 1982). Over harvesting was not identified as a problem until 1986 when concerns were voiced about some of the public grounds. State shellfish grounds were established and management measures including rotation schemes and shortened seasons have restored these resources. Oyster populations in leased areas are normally more than adequate to meet supplies (Pers. Comm. Anderson 2005).

Georgia and the East Coast of Florida - Pollution closures and development impacts have eliminated a large portion of the oyster harvesting areas in Georgia and on the east coast of

Florida (Cowman 1982, Ingle 1982). In 1981, only three harvesters were licensed in Georgia and one shucking house was in operation (Cowman 1982). Many of the estuarine systems on Florida's northeast and central coasts support oyster populations, but there is only an opportunistic fishery, with only a small percentage of the state's landings coming from these areas (See Section 3.4).

Gulf of Mexico

Oyster production in the Gulf of Mexico has been highly variable largely as a result of fluctuating environmental conditions. Louisiana produces most of its oysters on leases while in other Gulf States the grounds are nearly all public. Florida and Alabama only allow tongs for oyster harvest on public reefs. Mississippi, Louisiana and Texas allow harvest with dredges. Florida, Louisiana, and Texas are the only Gulf States that market oysters year round. Most oyster resources in the Gulf are subtidal and exhibit good sets and fast growth. Landings gradually increased during the 1960s and 1970s peaking in the early 1980s, declined in the late 1980s (drought from 1986-1989), and steadily increased after 1993. Confusion regarding the potential health risks associated with the consumption of raw oysters has eroded consumer confidence, which may affect oyster markets. Loss of habitat is perhaps the most serious and chronic problem facing the Gulf oyster industry. Oyster reefs and reef shell have been lost due to fishing disturbances, shell removal, and development activities. Cultch planting has been important in maintaining productive oyster reefs. Seed and direct harvest areas have been shelled. Other activities that conflict with oyster reefs are shrimp trawling, oil and gas facilities, channelization, and freshwater diversions. Hurricane tidal surges have buried and scoured oyster reefs and changed or removed protective barrier islands (Dugas et al. 1997).

West Coast of Florida - Harvest from public grounds accounts for 90-95% of Florida oyster landings. At least 90% of this harvest comes from Apalachicola Bay (Ingle 1982), which contains the state's most commercially valuable oyster reefs. Surveys of oyster populations were conducted in Apalachicola Bay as early as 1895 and intermittently until the present, and the commercial oyster industry in the city of Apalachicola was first described in 1881 (MacKenzie et al. 1997). About 600 acres of submerged lands in Apalachicola Bay are privately-held oyster leases, accounting for about 10% of the productive oyster habitat in the bay. Oyster production from Florida's Gulf Coast has been variable since the 1960s, ranging from about 1.5 to 6 million pounds of meats. Florida's oyster landings generally reflect Gulf-wide production levels and trends. Florida oyster landings declined in 1986 due to the impacts of Hurricane Elena on Apalachicola Bay in 1985 and poor production extended into 1992 due to drought conditions from 1987 through 1989. Oyster abundance increased in 1993 but low demand limited harvests (Dugas et al. 1997). The 2002 oyster assessment indicated an abundance of market-sized oysters in Apalachicola Bay and suggests that the oyster resource there is underutilized (Arnold and Berrigan 2002). Florida oyster managers developed a scale to determine the relative condition of oyster resources based on production estimates from oyster bar harvest areas. A production estimate of 400 bags per acre indicates a healthy bar capable of sustaining commercial harvest while an estimate of 200 bags per acre indicates that harvests should be limited. Oyster resources are considered depleted when stocks are below 100 bags per acre (Marsh 2004). Catch per unit effort in the oyster fishery dropped from 1986 to 1988, stayed low until 1991, increased and remained at relatively high levels until 1997 when it began another decline (Marsh 2004).

Florida began cultch planting on public reefs as early as 1914 and has maintained an oyster resource development program since 1949 (Dugas et al. 1997).

Alabama and Mississippi - Over the long term Alabama and Mississippi combined to produce about 12% of the total Gulf oyster landings. The two states suffered dramatic declines in production in 1987 that lasted until 1992 (Dugas et al. 1997). Landings in Alabama returned to long-term averages after the decline; however, Mississippi's landings increased to the highest levels in 30 years (NMFS Landings Data).

Louisiana - Oyster production in Louisiana has historically come primarily from leased bottoms (Berrigan et al. 1991), although public oyster grounds exhibited sizable increases in production during the 1990s and early 2000s (LDWF 2005). Lease acreage expanded from less than 50,000 acres in 1960 to around 330,000 acres in 1988 (Berrigan et al. 1991). CPUE data do not indicate a strong trend and effort remained stable from 1961 to 1986 (Berrigan et al. 1991). The public grounds in Louisiana are used as seed areas for the leases and for harvest of market oysters. Harvest of market oysters from public grounds has increased since 1992 and exceeded lease harvest in 1996 and 2002 (LDWF 2005). Long-term population abundance data indicate the Louisiana stock was stable at relatively low levels from 1982 to the early 1990s, increased until 2001 and declined during 2002 to 2005 (LDWF 2005). The 2005 oyster stock availability of 2,676,797 barrels (~12 million bushels of seed and market oysters) is the lowest since 1992 but still higher than all but one of the 1980s estimates. The Louisiana Wildlife and Fisheries Commission uses oyster stock availability data along with recommendations by the Louisiana Department of Wildlife and Fisheries – Marine Fisheries Division and the Louisiana Oyster Task Force to set the oyster season. Lower stock availability typically results in a shorter season (Pers. Comm. Banks 2005).

Texas - The Texas oyster fishery is comprised of two components: the public reef fishery and the lease fishery. Leases are found only in Galveston Bay and are utilized as depuration locations for oysters transplanted from restricted waters only. Lease harvest comprises 20-25% of the total commercial landings in Texas. Long term data indicated a general decline in oyster landings in Texas waters from 1956 to 1981, an extremely large increase in 1982 followed by another decline in landings until 1987 (Quast et al. 1988). Since 1987, the trend in landings has continued to increase to over 5.5 million pounds of meats harvested in 2004 (Campbell and Butler In press). Over half of the state's oyster public reefs are found in Galveston Bay, which account for 80% or more of Texas' annual commercial oyster harvest.

Fishery independent sampling from 1984-2003 indicates an increasing trend in catch-per-unit-effort (Martinez-Andrade et al. 2005) of market-size oysters (>75 mm) that generally mirrors the fisheries dependent landings trend over the same time period (Campbell and Butler In press). Catch-per-unit-effort of small (26-75 mm) oysters indicates a slight increasing trend during the 1984-2003 time period (Martinez-Andrade et al. 2005).

Canadian Maritimes

In Canada, eastern oysters are restricted to the shallow bays and estuaries of the southwestern Gulf of St. Lawrence and the coves of Cape Breton's Bras d'Or Lakes. Water temperatures in this area are warm enough to support species normally found much farther south because the estuaries have extensive shallow zones and broad intertidal flats, many with brightly colored sediments that absorb much radiant energy (Jenkins et al. 1997). The potential for overutilization of this resource is great due to extended growout periods of between four and seven years to reach market size and intermittent spatfall failures due to local waters not reaching spawning temperatures (Lavoie 1982). The early history of eastern oyster landings in the Canadian Maritimes is similar to many East Coast states with peak landings occurring around 1890 followed by a period of declining harvests. Failure to conserve seed oysters and shell, disease, and habitat impacts contributed to the decline that bottomed out around 1920. Peak oyster landings were around 87,000 bushels in 1890 while the lowest landings were about 7,000 bushels in 1920 (Jenkins et al. 1997).

Conservation measures started with a closed oyster harvest season in 1864 and an oyster size limit and culling regulations in 1920. All oyster harvesting on public beds is limited to hand harvest methods. Malpeque Bay disease had a pronounced effect on oyster stocks in Prince Edward Island from 1915 until disease resistant oysters began to allow increased production in 1940 and in New Brunswick and mainland Nova Scotia between 1954 and 1957 (Jenkins et al. 1997; DFO 2005a). In 1972, after another period of declining landings, the provincial and federal fisheries agencies began a program to rehabilitate the oyster fishery. Rehabilitation measures included cultch planting, cleaning natural shell beds fouled with sediment, and transplanting oysters for public harvest (Jenkins et al. 1997). Oyster landings responded and except for a short period from 1991-1993 have stayed at relatively high levels (Canada Department Fisheries and Oceans (DFO) landings data). Approximately 50% of the Canadian Atlantic oyster crop comes from lease areas where fishermen primarily utilize relaying of polluted wild stock as the means of production (DFO 2005a). The eastern oyster is not among the 67 aquatic species protected under Canada's Species at Risk Act (DFO 2005b).

Canada's annual production of approximately 25,000 bushels of eastern oysters is marketed primarily in Montreal and Quebec City and very few are exported. Demand exceeds supply creating a relatively high price for these high quality shell stock oysters (DFO 2005a).

East Coast of Mexico

Mexico's oyster harvest ranks sixth in the world and annually produces around one million bushels. Approximately 90% of the harvest is eastern oysters produced along the Gulf of Mexico. Economically it is the most important fishery in Mexico and virtually all of the harvest is marketed within the country for raw consumption. Eastern oysters grow in large shallow lagoons all along the east coast of Mexico in depths that seldom exceed two meters (6.5 feet) (MacKenzie and Wakida-Kusunoki 1997).

Oyster production is based on market demand and is not limited by supply. Fishermen's cooperatives control the harvest and in some areas control the beds where harvest can occur (Haro et al. 1982). The federal government imposed rules to protect the oyster resource in 1976. All harvesting is done by hand gear or by hand. Each harvest boat or dugout must have a harvester and a culler to return shells and small oysters to the beds as they are harvested. Also, no more than 20% of the oysters can be marketed in the shell because those shells are rarely returned to the beds. If more than 20% is sold in the shell, the cooperative must buy shells from another area and plant those shells on the beds. Oyster shells cannot be sold for other purposes (MacKenzie and Wakida-Kusunoki 1997).

Mexican lagoons receive regular abundant spatfall and the spawning season runs from March through October. Growth rates are high with most oysters reaching a harvestable size of 70-75mm (2.75-2.95 in.) in eight months. There are high mortalities of eastern oysters in most areas at one year of age and 76mm (3 in.) or greater in shell height. Only one survey for *P. marinus* has been conducted and infection levels were high in the area surveyed (Burreson et al. 1994). It is suspected that *P. marinus* is prevalent in the other lagoons as well. Impacts from red tides, oil pollution and outbreaks of illness from poor sewage treatment near oyster harvesting areas also affect availability and demand for oysters (MacKenzie and Wakida-Kusunoki 1997).

The management of oyster beds is under control of the fishermen's cooperatives. The harvest procedure consists of fishermen harvesting an entire bed over a period of several weeks or months. Stored shells are then spread on the bed for cultch and fishermen move on to the next bed. Oysters on the planted bed will be ready for harvest in 6-12 months and will be of relatively uniform size suited for the prevalent cocktail and half shell trade (MacKenzie and Wakida-Kusunoki 1997).

Oyster spawning and growth characteristics, management provisions, and habitat restoration activities appear to be effectively protecting Mexico's oyster populations from overutilization. Local observers feel that increasing cultch planting and expanding aquaculture could expand the Mexican oyster industry. Also, with better shellfish sanitation and/or depuration, oysters could be exported to the United States and other countries (MacKenzie and Wakida-Kusunoki 1997).

Bycatch

Bycatch was not discussed in any of the references used in this section. Oysters could be harvested in shrimp and crab trawls if these gears were towed over oyster reefs, but their design would not allow significant capture. Mechanical methods for clam harvesting will readily take oysters, but this type of gear is not normally allowed on oyster rocks because of the damage it causes to the habitat. Fishing gear impacts on oyster populations are more appropriately a habitat degradation/loss issue (Berrigan et al. 1991; Chestnut 1955).

Recreational Utilization

There is very little data on recreational oyster harvesting. The 1988 Texas Oyster Fishery Management Plan presents data that indicate the CPUE for recreational harvest was 0.3 kg (0.66 lbs.) of oyster meat per hour from 1983-1986. During the same period the average annual coast wide landings were 5,300 kg (11,684 lbs.) of meat (Quast et al.1988). Effort increased each year of the survey rising from 19,610 to 23,730 man-hours per year (Quast et al. 1988). Recreational oyster fishing activity was relatively low compared to finfish fishermen (Quast et al. 1988). Berrigan et al. (1991) concluded that it is likely more people have become involved in noncommercial oyster fishing in the past ten years due to variable market supplies and increased prices. No recreational harvest data was available. In North Carolina, recreational harvest of oysters is considered to be significant in some areas and was considered a factor in intertidal oyster declines in the 1960s, but there is no data (NCDENR 2001).

At least seven of the Atlantic and Gulf coast states have license requirements for recreational oyster harvesting. Daily catch limits typically range between 100 oysters and two bushels of oysters (NCDMF unpublished data).

Summary of Overutilization Assessment

The eastern oyster's life history characteristics of high fecundity, multiple spawns per season, very early age at maturity, fast early growth, wide salinity and temperature tolerance, and ability to colonize a wide variety of habitats make the species inherently resilient to natural and man-induced mortality (Marsh 2004). These survival advantages are most prevalent along the South Atlantic coast and Gulf of Mexico where oysters grow to harvestable size in one or two years and have a six to eight month spawning season. Fast growth quickly replaces lost habitat and allows oysters to reach harvestable size before disease effects occur. Protracted spawning seasons increase the likelihood of recruitment success by providing more opportunities for larvae to encounter suitable environmental setting conditions by avoiding freshets and high turbidity caused by storms. The advantages are diminished at the northern end of the range where eastern oysters can take four to seven years to reach market size and the spawning season decreases to four to six weeks or less in New England and the southwestern Gulf of St. Lawrence (Powell et al. 1994; DFO 2005a). Nonetheless, oyster populations in northern latitudes still exhibit remarkable resilience (Jenkins et al. 1997).

The Atlantic coast south of Cape Lookout and through the Gulf of Mexico appear to have avoided some of the extremely heavy utilization experienced by the area from Pamlico Sound to Long Island Sound. They were the last regions to reach historical peak oyster landings, and the intertidal oysters in this region were considered an inferior product and not harvested extensively at least until the early 1900s when canneries opened in the area. Harvest parameters in the Gulf of Mexico are currently less restrictive than those in the mid Atlantic area, but oyster populations there appear to be effectively managed and monitored so that harvest impacts are not substantial (Marsh 2004).

Eastern oyster resources from Pamlico Sound to Long Island Sound appear to have suffered from long-term overutilization. Negative impacts from disease, pollution and non-fishing habitat losses are also major contributors to current low population levels. State managers in this region have attempted to protect public oyster stocks by conducting stock assessments, setting conservative harvest quotas, lowering daily catch limits, limiting harmful gear use and reducing harvest seasons. Attempts to restore oyster populations and rebuild the resource through general cultch planting, reef rebuilding and oyster sanctuaries/reserves are also becoming common management tools in this region. Oyster managers struggle with balancing the needs of the resource and the desire to preserve the industry.

Oyster resources north of Long Island Sound are relatively small in comparison to other regions and much more susceptible to harvest pressure and environmental disturbances. Both of these causes had significant effects on oyster populations in this region. The Canadian Maritimes area maintains a small but persistent oyster fishery based on wild stocks and utilizes conservation measures similar to the mid Atlantic region. Wild harvest fisheries in the states north of Cape Cod declined very early and have been very low since the mid 1900s. Imported seed oysters were used in attempts to revive oyster production in this area but they failed and the oyster industry is now based largely on use of hatchery-reared stocks.

Even though oyster harvests are at or near record low levels along the majority of the U.S. Atlantic coast, resource managers and independent experts surveyed by the BRT indicate that overutilization (overharvesting) is currently a minor threat to extant oyster populations, occurring only seven times in 286 threats listed for the 71 estuaries assessed by respondents. It is important to note that survey responses identified current threats to oyster populations and that historical decline may have been caused by practices that are not current threats.

4.3 Predation and Disease

Predation

The planktonic life stages of the oyster (free-swimming trochphore/ veliger) are subjected to predation from a myriad of filter feeding organisms from rotifers to ctenophores (comb jellies and sea walnuts). Soon after the spat cements itself on or near the bottom, it becomes part of the benthic food chain. A variety of crab species are known to forage on oyster tissues. As oysters grow and their shells thicken, they become better able to withstand predation. However, some species such as carnivorous gastropods (e.g., drills, conchs and whelks) are able to prey upon oyster populations on both the Atlantic and Gulf coasts, and star fish are a common predator in coastal locations. Populations in the upper regions of estuaries are protected from many of these higher salinity predators. Flatworm turbellarians of the genus *Stylochus* have inflicted significant damage to estuarine oyster populations on both the Atlantic and Gulf coasts as well. A number of fish species such as black drum and cownose rays occasionally cause extensive damage to oyster beds, and diving ducks have also been documented as consumers of oyster tissue (Galtsoff 1964). Black drum have been documented to heavily impact seeded oyster reefs in Louisiana in both spring and early fall (Brown et al 2003). Early post-settlement mortality up to 99% occurs for many reasons. Competition for space with other oysters will also reduce the total oyster population. As stated previously, the environmental plasticity of the oyster enables it to grow and thrive under conditions that might be considered extreme to other species. Oysters exist from deep, high salinity waters to intertidal flats where they are exposed to additional predators during low tide. Predation varies with surface roughness (i.e., interstitial space) of habitat, with predation rates being higher in areas with low relief (Luckenbach et al. 1999).

There are many commensal organisms that make up a healthy oyster reef community. While many of these species reside on the outer surfaces of the oyster's shell, some species such as boring sponges and clams and mud worms, perforate the inner shell surface causing the oyster to expend extra energy maintaining the integrity of the shell cavity. The boring sponge, *Clionoa celata*, occurs in the Atlantic, while boring clams affect oysters in both the southern Atlantic and in the Gulf of Mexico. A number of mud worm species in the genus *Polydora* infest the shells of oyster populations on both Atlantic and Gulf coasts (Galtsoff 1964). Many of these infestations are natural associations and in general, most oysters survive. Thus, these associations do not seem to be having an effect at the population level.

Infectious Oyster Disease Agents

The following diseases are recognized by the World Organization for Animal Health (OIE). OIE members have strict regulations on export of diseased oysters or product in order to reduce the spread to regions not presently infected by these organisms. Locally, the threat posed by disease is reduced by not moving infected seed between states. However, intrastate movement still occurs. Preventing accidental introductions and controlling vectors of introduction (e.g., ballast water) are of critical importance to reducing the spread of disease organisms.

DERMO is a parasitic disease caused by *Perkinsus marinus*, which is a protozoan. The first major oyster pathogen to be identified was *P. marinus* (Levine 1978 = *Dermocystidium marinum;* Mackin et al. 1950 = *Layirinthomyxa marina;* Quick and Mackin 1971). Dr. John Mackin applied the first modern histological methods to describe a parasite (still referred to as DERMO disease) associated with summer oyster mortalities in Louisiana and Virginia that had occurred in the late 1940's. Later he showed, with histological sections of oyster tissues, the direct relationship of pathogen intensity and the death of the oysters (Mackin 1951). At the same time Drs. Willis Hewatt and Jay Andrews initiated their studies of oyster summer mortalities in Virginia and found wide spread oyster mortalities associated with this new pathogen (Hewatt and Andrews 1954; Andrews 1955). For over 50 years, studies have continued to document the impact of this disease organism. The parasite infects oyster in the first year of life and continues to proliferate causing up to 50% mortalities in oysters carrying the infection into their second summer season and 80-90% mortalities by the third year. Very few oysters that are infected with this disease organism survive a forth season. This parasite inhabits the immune cells of the oyster and perhaps suppresses the immuno response. It reduces the effectiveness of the oyster phagocytes; thereby, overwhelming the oyster's system and rendering it unable to fight off other opportunistic organisms.

Perkinsus marinus continues to cause significant mortalities along the Gulf and Atlantic coasts. Quick (1977) reported the range of *P. marinus* to be Massachusetts south to the Gulf of Mexico. Kern et al. (1973) reported the presence of *P. marinus* in eastern oysters introduced into the waters of Pearl Harbor, Hawaii. More recent reports extend its range from Maine (Burreson and Ragone-Calvo 1996; Ford 1996) to the Yucatan Peninsula (Burreson et al. 1994). Movement of infected seed oysters has resulted in the expansion of its range in the Chesapeake Bay. Sporadic reports of higher than normal mortalities occur from year-to-year within this reported range (Brousseau et al. 1998; Lewis et al. 1992). Reports of *P. marinus* in New England and Maine are probably the results of the movement of infected seed oysters. It has been generally accepted that cold conditions reduce the impact of, and unless there is extensive global climate warming, these northern extensions are not likely to remain. Conversely, should warming conditions persist, than one would expect to see even greater impacts on oyster populations throughout its range. High salinity and high temperatures elevate disease levels particularly during times of drought (Burreson and Andrews 1988).In addition to information presented to the BRT on the genetic variation reported between Atlantic and Gulf Coast oysters, there are reports of variation in pathogenesis and environmental tolerance in localized populations of *P. marinus* (Bushek and Allen 1996) and population variations in oyster disease resistance to DERMO (Gaffney and Bushek 1996) (See Section 7.1).

Decades of studying *P. marinus* have provided significant information. Early partial culture provided easy diagnostic capabilities (Ray 1966). A number of techniques have been developed to propagate the histozoic stages of this parasite; thus, allowing in depth studies of its physiological needs, life cycle stages, other growth characteristics. *P. marinus* can withstand a wide range of temperatures and salinities. The parasite has a direct life cycle with infective stages passing from one oyster to the next via the water column. The most likely method of disease transfer is via the movement of infected oysters. Once a population is infected it will spread from oyster to oyster. Peak mortalities occur during the summer period when higher temperatures and salinities provide the optimal conditions for parasite growth. Efforts to deal with DERMO have been focused on managing for the harvest of the oyster rather than managing the oyster's response. Because of the chronic nature of this parasitic disease, populations of oysters have the opportunity to spawn the first summer and others may be able to spawn a second or third time before succumbing to an infection.

MSX is a protozoan disease caused by *Haplosporidium nelsoni.* This second lethal disease was first reported in oysters from Delaware Bay. Extensive mortalities were observed in the fall of 1957 with massive mortalities occurring in the spring of 1958 and an unidentified organism first dubbed "MSX" for **M**ultinucleate **S**phere **X** (unknown), was associated with the dying oysters (Haskin et al. 1966). They reported oyster losses as high as 80% in some areas, killing both adult and juvenile oysters. Sindermann and Rosenfield (1967) reported oyster production in Delaware Bay fell from about 7.5 million pounds of shucked oyster meats prior to 1957 to less than 100,000 pounds by 1960. The parasite did not remain restricted to Delaware Bay; by 1959 the impact of the disease was reported in the Virginia and Maryland waters of the Chesapeake bay (Andrews 1966). A concerted effort by state, university and Federal agencies lead to the identification of spore stages (Couch et al. 1966), and MSX was eventually identified and named *Minchinia nelsoni* (Haskin, Stauber and Mackin 1966) and later reclassified as *Haplosporidium nelsoni* (Perkins 1990). The mid-Atlantic region still suffers from the heaviest impact from MSX along the Atlantic coast, even though it has been reported from Maine to Florida. Range expansion is probably due to the movement of infected seed and/or the natural movement or transplantation of a yet unidentified alternate host. Since first being reported, MSX has continued to be present in Delaware and Chesapeake Bay. The distribution and intensities of mortalities fluctuate from year to year mostly related to local salinity increases, brought on by drought conditions (Barber et al. 1997). MSX has recently reported to have invaded Maritime Canada (Stephenson et al. 2003) and has been documented in oysters from the Gulf of Mexico (Ulrich pers. comm. 2006). In a recent study, researchers were able to isolate and sequence *H. nelsoni* DNA from oysters that were collected from the Gulf of Mexico over the last 10 years. While the parasite has been in the Gulf for at least five to 10 years, it has not triggered an epizootic in the region which leads to questions regarding its intensity and the host-parasite relationship in subtropical latitudes (Ulrich pers. comm. 2006).

Unlike *Perkinsus sp*, *Haplosporidium nelsoni* has never been cultured. It is not transmitted directly for one infected oyster to another. By studying populations of infected oysters, it is now known that to sustain infections in an oyster population, the salinity must consistently be above 15 parts per thousand (ppt). This parasite infects, proliferates and kills the most oysters in areas where the salinity is generally above 18 -20 ppt. Proliferating parasites overwhelm the tissues of the oyster, resulting in a watery, emaciated individual that normally does not survive the infection. With heavy infections occurring in late summer, death is rapid. The time of infection to mortality is about six weeks. At sublethal levels of infection, the parasite interferes with the oyster's metabolism, its natural defense mechanisms, and reduces fecundity (Barber et al. 1988a, 1988b). Some oysters might not get a chance to spawn because MSX can kill zero year class juveniles before they have a chance to spawn. Initial infections occur in mid to late summer, with mortalities continuing until cooler waters slow metabolism of both the parasite and oyster. Heavily infected oysters may continue to die slowly over the winter period, and as water temperature rise in the spring, another period of mortality may occur.

During drought years the impact of MSX is even greater, exposing oysters that normally live in lower salinity conditions to salinities that support infections by MSX. Infected oysters transplanted to new locations can initiate infections that are sustained in those populations. Shellfish managers have restricted the movement of oysters from areas of high infection to areas not known to be infected. Many believe that because it cannot be directly transmitted that an alternate or intermediate host is needed to maintain infections and spread the disease within a given oyster population. As drought conditions wane, survivors and their progeny may reproduce to re-establish oyster populations. During the wetter years that occurred during the 1970's, there was significant recovery of oyster populations that had been devastated during the 1950-1960 MSX epizootic in both Delaware and Chesapeake Bays. Oyster recovery management programs have concentrated on moderate to lower salinity areas that are less likely to support the development of oyster diseases.

There is growing evidence that this parasite is an invasive species introduced to the East Coast of the United States in one of the many tests to introduce the Pacific oyster (*Crassostrea gigas)* for aquaculture development. Recent molecular techniques (Burreson 1997) have shown that *Haplosporidium* parasites in Pacific oysters from Korea (Kern 1976) and Japan (Friedman 1996) were genetically identical to *Haplosporidium nelsoni* from Virginia.

Malpeque Disease of Oysters is restricted to Atlantic Canada. It is limited to high salinity areas in southwest Nova Scotia and has not been reported in Bras d'Or Lakes, Cape Breton. The cause of the disease is unknown, but naïve oysters unexposed to the disease demonstrate up to 99% cumulative mortalities. Mortalities were first reported by Needler and Logie (1947) and later confirmed by Drinnan and Medcof (1961). Populations of oysters surviving the initial disease exposure are resistant to the disease and so are their progeny. Repeated testing shows continued presence of the disease and its ability to kill susceptible oysters, with no apparent disease in the existing oyster populations. Canada has restricted movement of oysters from these areas to prevent further spread to uninfected oyster populations.

4.4 Regulatory Mechanisms

Regulatory mechanisms for eastern oyster are most logically defined as habitat resource protection (preventative measures), fishery-specific, and conservation/replenishment based.

Habitat measures are those defined at the federal, state or local level designed to protect aquatic resources (including benthic reef habitat and water quality) from various direct or indirect development impacts (e.g., impacts of channel dredging, onshore development, point-source runoff, etc.). Harvest measures are those intended to control or regulate the commercial or recreational catch of the species, and may or may not be resource conservation based. Conservation/replenishment measures are those intended to ensure the continuance of the fishery or habitat resource through various measures including setting aside no-harvest areas, requiring culling of shell during harvest, setting up programs to return shells from harvested product back to reef areas, or natural seed movement programs intended to support either habitat or fishery restoration. Additionally, the state shellfish control agencies are responsible for managing shellfish harvesting areas for public health protection, which may result in permanent or temporary closures due to the presence of toxic algal blooms, elevated fecal coliforms and/or *Vibrio* spp., or chemical contamination. These restrictions may have the ancillary benefit of protecting some populations in chronically contaminated areas from harvest.

Federal

Throughout its range, the eastern oyster is not a federally managed fishery. Therefore, few federal regulations specifically address regulatory or management issues dealing directly with the eastern oyster. Oysters are primarily found in relatively shallow inshore locations. Thus, permit-requiring activities requiring consultation under Section 404 of the Clean Water Act or Section 10 of the Rivers and Harbors Act often involve the U.S. Army Corps of Engineers as the lead review agency, with various other federal agencies (typically NMFS and the U.S. Fish and Wildlife Service) providing resource protection recommendations. The Essential Fish Habitat consultation requirements of the Magnuson-Stevens Act and the Fish and Wildlife Coordination Act are intended to give each of the above listed federal resource agencies a mechanism to conserve and protect oyster reef habitat.

State/Local

An exhaustive compendium of all state and local management tools is beyond the scope of this report. However, a brief overview of state and local regulations will be covered in the following sections.

Resource Protection

Similar to the regulatory process identified at the federal level, most states have a parallel environmental review and permitting process intended to protect nearshore aquatic habitat (including oyster reefs) from a variety of potential impacts. Individual states are delegated the authority and responsibility to enforce the provisions of the Clean Water Act pursuant to Section 401 by regulating discharges into the nearshore environment.

Harvest/Fishery Management

Oyster harvest management is not typified by any consistent strategy or rule throughout the range. Overarching harvest regulations, specifically the opening or closure of some sites or the entire fishery, are based upon maintaining some degree of sustainability. More often, however, harvest regulations are centered more around controlling the daily harvest totals, effort, or efficiency (via gear restrictions). Few if any areas have harvest quotas that are defined based on any population census (fishery independent) data. Seasonal restrictions on harvest enacted in most states are not so much intended to promote or protect stocks of oysters during spawning, but rather have more to do with the marketability of the oyster when energy is diverted to gonadal tissue, reducing meat quality.

Throughout the range, oyster habitat and oyster growing areas are variously classified as public grounds and private (or lease) grounds. Public grounds can be closed, open for recreational and/or commercial harvest, allow specific types of gear, have various minimal (and occasionally maximum) cull sizes, or other site-specific measures. In most areas the goal is to promote the sustainability of the commercial fishery, but resource conservation benefits are realized secondarily. Limiting gear type to less efficient gears (e.g., hand tonging) tends to reduce the economic viability of harvesting all available product, which helps to promote the maintenance of some standing stock on public grounds. Additionally, limiting the use of very efficient gear (such as large, powered dredges) that can significantly impact oyster reef habitat, limits the long-term impacts of harvest and helps to promote sustainability of the habitat.

Privately held submerged lands and sovereignty submerged lands (leased grounds) typically have far fewer constraints as to regulations or restrictions on site-specific production, harvest, seasonality, or conservation/replenishment requirements. Most states, which lease submerged lands, apply specific terms and conditions to the use of those areas.

Conservation/Replenishment

Specific conservation and replenishment measures (as opposed to indirect results of fishery management measures) vary among states, and not all states have measures in place. Some states or localities have harvest surcharges that fund replenishment of historic bottom via cleaning of bars, relocation of buried shell, or the purchase and re-planting of shell initially removed as part of the fishery harvest. Virtually all states require all barren shell brought up as by-catch to the harvest be replaced back on the bottom. Other states have voluntary or mandated buy-back programs whereby processors are compensated for making harvested shell-by-product available to return back to productive bottom areas.

Beyond the indirect result that fishery closures (for whatever regulatory reason) have in terms of creating non-harvest or sanctuary areas, some states have enacted programs or regulatory processes whereby small, isolated or large contiguous areas are set aside as off-limits to harvest (NCDENR 2001). This strategy is typically done to maintain a broodstock reserve area, whereby larger, more fecund oysters are intended to be retained to allow natural re-seeding of adjacent areas. Less frequently, historic oyster reef areas have been set-aside principally as habitat sanctuary areas, where the primary focus of the site is for the oyster reef to serve as benthic community habitat. In either case, both oyster-specific and ecosystem-specific benefits may be realized.

There is conflicting information as to whether intentional bottom-disturbing activities (bar-cleaning, bagless dredging, suction dredging of sediments off of lightly buried shell, or the very act of harvesting and culling oysters via various gear types) benefits or impacts natural oyster reef habitat. Some advocates contend that this method cleans shell surfaces to allow a new settlement of oyster larvae, while others contend that these measures only result in additional destruction of three-dimensional habitat (Maryland DNR 2002).

International

Oyster resources in Mexico are managed by the Secretaria de Medio Ambiente Recursos Naturales y Pesca (SEMARNAP). In some areas of Mexico, the management of oyster beds is under the control of fishermen's cooperatives. The Canadian oyster resources are managed by Canada DFO primarily through seasonal and gear restrictions.

4.5 Other Natural and Manmade Impacts

Introductions (*C. ariakensis*)

The state of Maryland and the Commonwealth of Virginia have proposed to intentionally introduce a non-native oyster species, *Crassostrea ariakensis*, into the Chesapeake Bay and other state tidal waters. This species, which is native to Asia, appears to have greater resistance to the pathogens responsible for MSX and Dermo. However, little is known about the life history and ecology of *C. ariakensis* in its native range, and current information is insufficient to predict the impacts an introduction of *C. ariakensis* might have on the native *C. virginica* oyster.

In 2003 the U.S. Congress authorized the Army Corps of Engineers to prepare an Environmental Impact Statement (EIS) to examine both the risks and benefits of introducing this species to the Chesapeake Bay. The EIS is being conducted by the Corps as the lead federal agency, with the states of Maryland and Virginia serving as lead state agencies. The U.S. Environmental Protection Agency (EPA), National Oceanic and Atmospheric Administration (NOAA), and Fish & Wildlife Service (FWS) are cooperating agencies on the EIS.

In 2004 the NOAA Chesapeake Bay Office (NCBO) initiated a Non-native Oyster Research Program funded at $2M annually to obtain the scientific information needed to prepare a thorough EIS. The program is aimed at research priorities recently identified by the National Research Council (National Research Council 2004) and the Scientific and Technical Advisory Committee of the Chesapeake Bay Program (STAC 2004), as well as guidance from the International Code of Practice on the Introductions and Transfers of Marine Organisms (ICES Code of Practice). This 3-year, $6M research program is scheduled to complete all the highest priority research needs by the end of 2007.

Major research topics under investigation include:

1. Understanding *C. ariakensis* within its native geographic range
    a. Taxonomy, population genetics
    b. Pathogens
    c. Ecology, reef building, phenotypic variation

2. Potential for population growth and sustainability of *C. ariakensis* in Chesapeake Bay
    a. Demographic model

b. Larval transport model
c. Gametogenesis, fecundity, spawn cues, sex ratio
d. Fertilization efficiency coefficient
e. Larval temperature & salinity tolerances
f. Larval mortality
g. Larval physiology, behavior, metamorphosis
h. Settlement cues, substrate preferences
i. Juvenile mortality - mesohaline predation
j. Juvenile mortality - polyhaline predation
k. Juvenile/adult mortality - low DO, sediment
l. Growth rate
m. Triploids as surrogates for diploids

3. Susceptibility of *C. ariakensis* to known disease-causing parasites and pathogens
    a. *Bonamia* spp.
    b. Herpes virus and vertical transfer
    c. Other viral pathogens

4. Interactions between *C. ariakensis* and native oyster species
    a. Hybridization, gamete competition
    b. Competition (food, space, etc.)
    c. Spawning cues

5. Human consumption risk
    a. Fecal coliform uptake, clearance rates
    b. Viral and protozoan human pathogens
    c. Post-harvest pathogens levels

6. Potential for *C. ariakensis* to become a fouling nuisance
    a. Larval substrate preferences
    b. Fouling potential

7. Ecosystem services and functions
    a. Reef building
    b. Filtration and water quality
    c. Food web dynamics

8. Economic and cultural impacts

Possible risks associated with an introduction of *C. ariakensis* have been described by the National Research Council (2004). Risk factors that could affect *C. virginica* include:

Disease

- A new disease-causing organism might be introduced that would negatively impact *C. virginica*.

- *C. ariakensis* might serve as a reservoir for pathogens, thus increasing levels of infection for *C. virginica*.

Direct Interspecific Interactions
- *C. ariakensis* might out-compete *C. virginica* for limited hard substrates.
- Cross-fertilization could result in reduced reproductive success for *C. virginica* (i.e., gamete sink) or hybridization.

As the federal research program and EIS work continue, these factors will be evaluated to form a clearer picture of how *C. ariakensis* might impact native *C. virginica* populations in the Chesapeake Bay.

“Harmful” algal blooms (HAB)

Oysters, and other bivalve mollusks, were historically-characterized as “symptomless” concentrators of toxins produced by “red-tide” dinoflagellates. Sophisticated surveillance and management programs have been instituted worldwide to prohibit shellfish harvest when toxic algae have the potential to contaminate shellfish tissues (Shumway 1996). More recently, detrimental effects of some microalgal taxa, including but not limited to those that produce toxins that threaten human consumers of shellfish harvested during red-tide blooms, have become recognized (Shumway 1996; Landsberg 2002).

Over their extensive range, eastern oysters are exposed to several species of toxic or harmful algae, which tend to be more constrained geographically. In a north-to-south listing, the following HAB-oyster interactions occur; observed effects upon oysters are summarized:

Alexandrium fundyense, A. tamarense: This is the well-known, “New England red tide” alga; two species have been implicated, but these may be conspecific. This dinoflagellate produces a suite of neurotoxins (termed ‘saxitoxins’) that interfere with sodium-channel transmission of nerve impulses in exposed vertebrates (Kao, 1993). Clinical effects include loss of motor control and respiratory failure in extreme cases (Backer et al., 2003). Eastern oysters retain toxins produced by these microalgae while feeding and are able to tolerate relatively-high tissue concentrations without suffering direct mortality. A recent study demonstrated adductor-muscle paralysis in oysters exposed to cultured *A. fundyense* (Hégaret et al., submitted), but respiratory, feeding, and hemocyte functions remained unaffected. Thus, *A. fundyense* does not appear to be acutely-toxic to oysters, but adductor-muscle paralysis may leave oysters more susceptible to predation, as they are unable to close the shell. A recent report indicated, however, that at least some vertebrate predators (in addition to humans) avoid eating saxitoxin-contaminated oysters (Kvitek and Bretz, 2004).

Prorocentrum minimum: This dinoflagellate is a common bloom-forming species in coastal bays from New England through the Mid-Atlantic region. Production of mammalian toxins by this taxon is unclear, but no cases of human poisoning directly attributable to *P. minimum*-contaminated shellfish have been confirmed (Landsberg, 2002). *P. minimum* blooms – called “mahogany tides” in some places – have been associated with mass mortalities of oysters and other marine life (Heil et al., 2005). In some cases, environmental effects can be attributed to low dissolved oxygen following respiration of high-biomass blooms, but in other cases, direct toxicity was suggested (Grzebyk et al., 1997). Controlled laboratory studies have demonstrated acute and sub-lethal effects of *P. minimum* upon oysters and other mollusks (Wikfors, 2005); therefore, it appears likely that natural blooms impact survival, or at least health, of oyster populations. *P. minimum* blooms tend to be highly-localized and short in duration, and biological effects are dose and time-dependent. Thus, severe impacts are expected to be local and episodic.

Heterosigma akashiwo: This raphidophycean flagellate has been recognized as a killer of finfish for many years (Honjo, 1994), but effects upon oysters and other mollusks have been studied only recently. The taxon affects fish chiefly by causing gill-tissue damage when reactive-oxygen radicals on the cell surface contact gill epithelial cells as fish respire. As is the case with finfish, mollusks respond to *H. akashiwo* by avoiding contact or mucous production at the gills when respiration becomes necessary (Wikfors, G.H., unpubl. obs. 2004). The taxon also has been shown to produce toxins (Khan et al., 1997) generally associated with some dinoflagellate taxa (gonyautoxins – see below), but biological effects of these toxins in *H. akashiwo* have not been demonstrated. *H. akashiwo* blooms tend to be even more localized and episodic than *P. minimum*, thus, they present a minor threat to oysters capable of minimizing contact through shell closure.

Karlodinium veneficum: This dinoflagellate species (until recently, referred to as *K. micrum*) currently is emerging as an ichthyotoxic HAB in mid-Atlantic coastal bays and ponds (Deeds et al. 2002). Research in progress is showing biological effects of *K. veneficum* upon eastern oysters (Place, A., pers. comm. 2005), but the importance of this HAB in oyster habitats is not currently known.

Aureococcus anophagefferens: Distribution of *Aureococcus anophagefferens*, originally recognized only on the northeast coast of the US (Anderson et al. 1993), now is recognized along the entire Atlantic coast of the US from Maine to Florida (Gobler et al. 2005). The Atlantic "brown tide" alga, a member of the Class Pelagophyceae, has been shown to interfere with feeding in mussels, scallops, and eastern oysters, sometimes causing mortalities (Gobler et al., 2005). The hypothesized mechanism for effects in shellfish seems to involve an "anaesthetic" effect of *A. anophagefferens* cells on the ciliary motion by which bivalves move water through the gills for respiration and feeding (Gainey and Shumway, 1991). Mortalities appear to be a consequence of hypoxia in the palial cavity as water is not renewed (Bricelj et al., 2001). Mortalities of oysters associated with brown tide blooms have not been reported, but the most-dense blooms have occurred in areas where bay scallops and Northern quahogs are more abundant; these bivalves have been shown to suffer mortalities (Gobler et al., 2005).

Pfeisteria piscicida and *P. shumwaei*: While not photosynthetic, these heterotrophic dinoflagellates generally are included in discussions of HABs. These species are thought to exist most of the time as predators on microalgae, and expression of toxicity and/or predation on fish and shellfish according to environmental cues not completely understood. Recently, predation of *Pfeisteria* cultures upon molluscan larvae has been demonstrated in the laboratory, and *Pfeisteria* cultures have been shown to prey on post-set shellfish (Springer et al. 2002). Blooms of predatory *Pfeisteria* populations are relatively rare, considering that the species is present over much of the eastern oyster's range. It appears that a narrow set of environmental cues is necessary for these species to express behaviors that make them a threat to bivalve mollusks (Burkholder and Glasgow, 2002).

Alexandrium monilatum: *Alexandrium monilatum* is widely distributed in tropical and sub-tropical waters of the Gulf of Mexico and the southern Atlantic coast of North America, with reports of occurrence as far north as the Chesapeake Bay (Balech 1995). This dinoflagellate has very recently been recognized as ichthyotoxic, causing mortality in oysters and other mollusks (Pate, S. pers. comm. 2005); therefore, the environmental importance of oyster trophic interactions with this HAB are not fully understood.

Karenia brevis: Contamination of oyster tissues with brevetoxins (previously referred to as 'gonyotoxins') from the "Florida red-tide" dinoflagellate make oysters unfit for human consumption, but symptoms of stress or dysfunction in oysters exposed to this species have not been described (Landsberg 2002).

Hurricanes

Coastal estuaries in the Gulf of Mexico and South Atlantic, and in the mid Atlantic Bight to a lesser extent, are subject to hurricanes and the extreme climatic, hydrological, and environmental conditions associated with the passage of these weather phenomena. Hurricanes, tropical storms and associated flood events are essential elements in estuarine ecology. Oysters are inhabitants of coastal estuaries, and their broad environmental tolerances and prolific reproductive capabilities make them well suited to endure these short-term natural phenomena.

Hurricanes have had devastating impacts on oyster production and its dependent economy (Engle 1948; Ford 1970; Berrigan 1988; MacKenzie 1997c; Perret et al. 1999). Turbulent hydrologic conditions associated with hurricanes may result in habitat loss and damage to oyster reefs through various mechanisms; including destruction of reef integrity, removal of live oysters, burial, scouring, abrasion, and freshets (Berrigan 1988; Dugas et al. 1997; Perret et al. 1999). The severity of damage is often exacerbated or mitigated by local conditions; including tides, storm surge and rainfall.

Extreme environmental, meteorological, and hydrological conditions associated with hurricanes are known to result in severe devastation to oyster reefs. Devastation includes losses or debilitation of oyster resources that may have short-term or long-term effects. Short-term effects may include loss of fishable stocks, disruption of recruitment, and loss of fishery revenues. Long-term effects may include the loss of all standing stocks, loss of recruitment, the cessation of fishing (harvesting), loss of reef integrity, and loss of reef ecology. There may be serious economic consequences for the dependent fishing community associated with both short-term and long-term impacts.

Extreme conditions can result in physical damage to reefs and oyster populations. Severe hydrological conditions such as storm surge and wave action can scour oyster reefs, kill oyster spat and juvenile oysters, physically remove oysters from a reef, as well as destroy the structural integrity of a reef. Oysters may be washed from the reefs onto water bottoms that cannot support oysters where they become buried in soft mud and sediment. Under the most extreme conditions an entire reef can be destroyed by scouring, erosion and subsidence. In these cases, generations of reef development may be lost. Intertidal reefs and shallow subtidal reefs are frequently more susceptible to severe hydrological conditions.

Excessive sedimentation over oyster reefs is also commonly associated with the severe hydrological conditions. The displacement of sediments and debris over oyster reefs results in burial and extensive mortality within oyster populations. Sedimentation results in long-term damage to reef integrity and functionality. It may take an extended period for sediments to erode from reefs, during which time oyster reproduction and growth are minimal.

Oyster mortalities may continue after the direct effects of hurricanes, as unfavorable environmental conditions may persist long after the storm has passed. A combination of stressors, including rapidly changing salinity levels and water temperatures, decreased dissolved oxygen concentration levels, and high concentrations of potential contaminants may contribute to oyster mortalities as long as the conditions persist. Additionally, increasing amounts of freshwater will drain into the estuaries as flood waters recede in the drainage basins throughout the region, and prolonged periods of reduced salinity levels may also contribute to continuous mortalities. When adverse conditions are prolonged, there is an increased likelihood that natural reproductive cycles, larval development and spat setting will be affected. Critical spawning and setting peaks may be interrupted, and disruption of these cycles may have impacts on oyster populations that continue for several years.

Oyster resources in the Gulf of Mexico have been directly impacted by a series of hurricanes in 2004 and 2005, including Hurricanes Charley, Ivan, Dennis, Katrina and Rita. These hurricanes adversely affected most of the productive shellfish growing areas from Florida Bay to Galveston Bay. All of the Gulf States are engaged in assessing oyster resource losses and economic impacts to the oyster fishery resulting from these hurricanes. Preliminary information suggests that oyster resource losses range from extensive ecological damage to short-term disruption in local fisheries. In almost every case, the levels of damage are commensurate with the severity of storm conditions encountered and the proximity of the affected estuary to the storms' path.

Following hurricanes, oysters will repopulate estuaries when environmental conditions stabilize and suitable substrate is available. Under favorable conditions, oyster production may even be enhanced as a result of nutrient inputs and the depression of marine predators which may be associated with flood events. Also, available substrate on existing oyster reefs may be enhanced by wave action and scour which acts to expose clean substrate when conditions are not too severe. Numerous reports describe the re-establishment of productive oyster reefs after populations were decimated by hydrologic events associated with storms and floods (Hofstetter 1981 1988; Berrigan 1988 1990; Perret et al. 1999). Full recovery of buried reefs is usually accelerated by restoration activities to enhance reef substrate.

5. Aquaculture

5.1 Cultivation and Aquaculture of Eastern Oysters

Oysters have been subjected to some level of "domestication" since the time of the Roman Empire, when oysters were held in coastal ponds for convenient harvest as needed (Clark 1964). In the Western Hemisphere, Native Americans harvested intertidal eastern oyster populations prior to European colonization, and access to sub-tidal populations in the northern portion of the species' range was limited by relatively-primitive harvesting tools – wooden rakes and tongs. Unsustainable harvest of natural oyster populations, enabled by importation of the dredge from Great Britain, led to declines in commercial production as early as the mid-eighteenth century in some coastal waters (Kochiss 1974). These declines led to directed efforts to increase the quantity and reliability of commercial oyster production (Belding 1912; Kochiss 1974). Two problems needed to be solved for effective management of oyster production: one was social – establishment of ownership of shellfish stocks in publicly-owned bottomlands, and the other was technical – improving recruitment of seed oysters.

As most waters from which eastern oysters were traditionally harvested are under state or municipal jurisdiction, these governmental entities were responsible for establishing programs by which individuals could have exclusive rights to shellfish populations. In states that established programs for leasing bottomlands (e.g., Connecticut, Massachusetts), shellfishers had motivation to cultivate beds (alleviate siltation and eliminate predators) and harvest sustainably. Nevertheless, most commercial production on leased bottomlands has relied upon natural settlement of spat.

Cultivation of oysters for human consumption is accomplished with a wide range of technological sophistication. The simplest form of oyster cultivation involves simply moving wild oysters from one place to another. Oysters can be collected in areas of high spat settlement or in waters closed to harvest because of sewage contamination and moved to bottomlands where sufficient growth and/or depuration occurs prior to harvest. When oysters are moved for purposes of depuration, this activity is generally referred to as "relay;" whereas, moving oysters for growth is referred to as "aquaculture." Relocation of young oysters to growing beds also generally involves adjusting the population density, or proximity of oysters to each other. The oyster farmer attempts to distribute oysters such that competition for phytoplankton food does not limit growth, but otherwise to optimize production within the confines of his lease. Planting of oysters directly on the bottom at relatively high density may attract predators, such as crabs and starfish, leading to high predation loss to the oyster farmer. Thus, the next level of technology applied to oyster cultivation is protection of the beds from predators. Although various techniques have been considered, practically speaking, "mopping" for starfish (dragging the bottom with cloth string arrays to which the spiny skin of starfish adhere and killing the starfish on-board the boat with hot water) and "potting" (trapping) of crabs are most-commonly employed.

In this context, production on leased beds of wild-caught oysters may not be considered "aquaculture," in the strictest sense, but rather resource enhancement through habitat modification.

One definition of domestication is:

> *"that process by which a population of animals becomes adapted to humans and to the captive environment by some combination of genetic changes occurring over generations and environmentally-induced, developmental events re-occurring during each generation."* (Price 1984)

Thus, as developmental events are not induced during each generation, cultivation and protection of naturally-spawned, unselected oyster populations can be considered population enhancement, rather than aquaculture. Some alteration in the genetic structure of oyster populations "amplified" by mitigation of "natural" loss terms in population dynamics (burial, predation) can occur if oysters that would have been thusly removed before reproducing are permitted to spawn. Nevertheless, ultimate harvest of these oysters immediately upon achievement of commercial size would minimize the effects of this type of "aquaculture" upon un-cultivated oyster populations, while increasing commercial production. If anything, this "aquaculture" activity reduces harvest pressure on unmanaged, natural populations. This type of cultivation of wild oyster populations accounts for most current, commercial aquaculture production in the Gulf and northeast Atlantic coast states.

Aquaculture production based upon "domesticated" breeds of oysters, selected and spawned in captivity on a continuing basis, is relatively new and small in scale (Committee on Nonnative Oysters in the Chesapeake Bay 2004), but provides a premium product, in terms of monetary value. The long-term investment in genetically-selected "breeds" of oysters and expense associated with captive breeding and rearing of seed justifies a greater investment in protection of livestock oysters being grown in captivity. Accordingly, on-bottom culture is being replaced by cage-culture technologies whereby predator exclusion is improved and cultivation (cleaning, moving) is facilitated. In regions where oysters achieve market size after first spawning, there is the potential for selected oysters to contribute to the gene pool of co-occurring, wild oyster populations; however, evidence from genetic analyses of populations on the Atlantic coast suggest that this has not occurred widely (Pers. Comm. Gaffney 2005). Further, reproductive isolation by culture of mainly sterile, triploid oysters – commercially motivated by faster growth rates – is increasingly being applied in oyster aquaculture (Baker 1996). Triploid oysters, whether produced by chemical induction or breeding of tetraploid males with diploid females, are extremely unlikely to contribute to the gene pool of local, wild oyster populations because gametogenesis and spawning of triploids is vanishingly rare.

In summary, oyster aquaculture is practiced in two forms: one based upon collection of wild spat that amplifies natural production for commercial harvest with minimal effect on the local gene pool, and another that represents true "domestication" and is essentially reproductively isolated from wild populations. The main effect of aquaculture activities on oyster population biology is to provide a reliable, sustainable commercial harvest unaffected by fluctuations inherent in reproduction and recruitment of wild oyster stocks.

6 Status of Population

In order to present information to assess the current status of eastern oyster populations throughout their range, quantitative and preliminary assessments for eastern oysters were reviewed and available information is incorporated below. However, the BRT determined that this information was insufficient to fully evaluate the status of the species. Thus, a survey was developed as an additional tool.

6.1 Quantitative Stock Assessments

Quantitative population models are typically used to determine the ability of fisheries resources to sustain themselves considering all the factors affecting their survival. This type of analysis has not been applied to oyster populations until recently most likely due to lack of in-depth studies on important life history parameters (Rothschild et al. 1994) and failure of state agencies to gather necessary data. Chesapeake and Delaware bays and the public oyster grounds in Louisiana were the only areas found to have recent quantitative assessments of oyster population status.

Rothschild et al. (1994) may have produced the first successful, modern attempt at applying well-established stock assessment techniques to analyze oyster population dynamics. They found substantial overfishing was occurring in Chesapeake Bay early in the 1900s and in 1990. Their efforts were complicated by a lack of in–depth studies on oyster size, growth, mortality, and reproduction (Rothschild et al. 1994). Jordan et al. (2002) analyzed Maryland oyster population data and found significant differences in age-length determinations that probably caused elevated mortality estimates by Rothschild et al. (1994). The Chesapeake Bay 2002 Comprehensive Oyster Management Plan contains recommendations to improve biomass-based, quantitative population models (COMP 2002). The Chesapeake Bay oyster fishery is classified as overexploited with a low/depressed relative abundance (Marsh 2004).

In one directed effort to conduct ongoing, quantitative stock assessment, the Haskin Shellfish Research Laboratory has been conducting oyster stock assessment workshops for the New Jersey Delaware Bay oyster beds since 1999 (HSRL 2005). The 2005 Stock Assessment Workshop report indicates that the market-size component of the oyster population is in a period of negative surplus production as a consequence of five years of low recruitment. This means that the market-size population of oysters is expected to contract in 2005 even in the absence of fishing. The harvest in 2004 was one of the lowest on record since 1953 (HSRL 2005). The report does not assign a stock status to the New Jersey oyster population; however, the management recommendations include establishment of specific management parameters conducive to stock rebuilding in times of surplus production including harvest limits for 2005 (HSRL 2005).

6.2 Preliminary Stock Assessments

States and regions involved in fishery management planning processes may be required to make determinations of stock status without the data necessary to conduct a complete population assessment. In this case the available fishery and biological data, or proxies for that data, are used in a preliminary population assessment. Delaware, North Carolina, Texas and the Gulf States Marine Fisheries Commission produced oyster fishery management plans with this type of assessment of oyster population status.

The Delaware Division of Fish and Wildlife uses a proxy based on the percentage of market oysters in the standing stock to ensure the sustainability of the State's oyster population. A projected harvest quota is established by analyzing the percentage of direct market oysters greater than 2.75 inches on five primary Delaware Bay oyster beds. The lower 95% confidence limit, average, and upper 95% confidence limit on the annual survey index of market oysters per bushel serve as harvest control thresholds. The use of these thresholds allows for protection of oyster populations even though age structure, recruitment patterns, or disease dynamics may be changing. Delaware Division of Fish and Wildlife is currently recommending use of the more conservative upper confidence limit due to several years of low recruitment and an anticipated oyster population decline in their portion of the Delaware Bay (DFW 2004).

North Carolina developed a fishery management plan for its oyster resources in 2001 and assigned a stock status of "concern" for the oyster population. Stocks designated as "concern" are those stocks for which an assessment is incomplete but that show from available data that overfishing is a threat. For the subtidal oyster populations in the Pamlico Sound region, the stock status factors causing concern were high *P. marinus* mortality, reduced spatfall, low CPUE, and suspected limited spawning stock. The intertidal populations in the southern part of the state showed evidence of high harvest pressure and significant habitat disturbance. Annual CPUE data are monitored to establish limits on the fishery. The oyster season is typically closed early in many areas due to depletion of harvestable oysters (NCDENR 2001).

The Texas Oyster Fishery Management Plan was completed in 1988. Stock status could not be determined but fishing effort was thought to be occurring at a level that exceeded optimum yield (Quast et al.1988). A further statement on the condition of the resource concluded that, at the time, oyster abundance levels could not support increasing fishing effort. Factors involved in this determination included: overall depressed oyster abundance on harvestable reefs, reduced spring spat settlement peaks, and poor survival of spat and small oysters due to fishing pressure (Quast et al. 1988). Galveston Bay was closed five times between 1979 and 1988 because oyster reefs in the area were determined to be overworked and damaged (Quast et al. 1988). There has not been an update of the Texas Oyster Fishery Management Plan since 1988 (Marsh 2004) and Texas Parks and Wildlife Department's participation in Gulf States Marine Fisheries Commission planning process provides more recent evaluation of the Texas oyster fishery. In order to help stabilize fishing effort, the 79th Texas Legislature (2005) established a moratorium on licenses in the Texas commercial oyster fishery; whereby, only those individuals holding a license on August 31, 2005 were eligible to purchase a license in subsequent years, and a license must be renewed each year to maintain eligibility. In conjunction with the license moratorium, the Texas Parks and Wildlife Commission reduced the daily limit of oysters from 150 sacks to 90 sacks per day (110 pounds per sack) in an attempt to lengthen the productive part of the season and provide for a more stable price structure for oysters taken throughout the duration of the open season.

"The Oyster Fishery of the Gulf of Mexico, United States: A Regional Management Plan" makes the finding that oyster abundance and range in the Gulf appear to be more limited by salinity/temperature regimes and available substrate for setting than fishing pressure (Berrigan et al. 1991). The plan goes on to state that overharvest may occur but that it is harvest above optimum yield only (Berrigan et al. 1991). Optimum yield is defined as:

> All the adult oysters of practical value and use that can be harvested from a given reef area provided: 1. The shell (or an equal or greater amount of other cultch material proven to be as effective as the whole oyster shells in catching and retaining spat) are returned to the reef in the same areas that harvest occurred; and 2. Freshwater from natural stream sources and runoff to the reef are maintained or restored in a manner that, a) eliminates contamination from harmful substances to the oyster or man (as a result of consumption) and b) optimizes salinity, temperature, water flow and nutrient conditions for oyster setting, growth and survival. (Berrigan et al. 1991)

Powell et al. (1994) compared resistance to mortality between oyster populations in Chesapeake Bay and Galveston Bay using a time dependent energy flow model and found the Chesapeake Bay population required more conservative management measures possibly providing one explanation for the difference in the status of oyster populations in the two areas.

6.3 Survey of Eastern Oyster Status

This survey (see Appendix II) was developed as a telephone questionnaire for resource managers and independent experts and was designed to elicit responses from these experts as they pertain to individual estuaries, or shellfish growing areas (SGA), throughout the species range. Respondents were typically identified by members of the BRT due to familiarity with managers and experts in each state. Twenty resource managers and independent experts responded to the survey with information that covered 72 estuaries throughout the range of the eastern oyster (Appendix III). Given the numbers of estuaries in some states, there were many cases in which a member of the biological review team discussed the survey questions with the resource manager or independent expert and then allowed for the survey to be filled out at the respondents' convenience. If necessary, the respondent was contacted to clarify any responses. The survey was meant to reflect the opinions of the respondent and may or may not reflect the official views of the agency or institution through which the respondent is employed.

Survey responses were sought from both a resource manager and an independent expert from each state so as to avoid any perception of bias in regard to survey results. For instance, a resource manager may have the perceived bias of showing only the benefits of successful oyster resource management, while an independent expert (often an academic) may have the perceived bias of discussing only negative aspects of the oyster status in order to justify additional funding for research. Opposing responses between the resource manager and independent expert would have highlighted any potential bias; however, responses elicited by the survey showed no trend of consistent bias between respondents for individual states or estuaries. There were a few questions which often resulted in different responses; however, these differences are easily understandable in light of the lack of information available on oysters. The following are some examples of- and likely explanations for- such differences:

- There were often differences in responses to the historic and current acreage present in each estuary but this often relies on best estimates and is highly dependent on the definition used to quantify such acreage. In some cases, acreage may be quantified as the total area available that could support oysters even if the presence/absence of live oysters is unknown.
- There were often differing responses to the question “What, if any, do you perceive as the primary threats to the oyster population in this estuary/SGA?” In this case, differing responses may not necessarily indicate a disagreement between the resource manager and the independent expert. For instance, if each respondent had been privy to their counterpart’s responses, they may have agreed; however, given the wide range of threats that could impact oyster populations, it would be unreasonable to assume that independent responses would be exactly the same.
- There were also differences in responses that seemed to be a result of a disparity in the information that each respondent had available to them. For instance, there were often differences in responses regarding the questions, “Has oyster restoration or enhancement work been done in this estuary/SGA?” and “If yes, is it conservation based or fisheries based?” One respondent might indicate that restoration was only fisheries based while the other respondent indicated that both conservation based and fisheries based restoration had occurred. In this case, it seemed most reasonable to conclude that differing responses were an indication that the first respondent was simply not familiar with the conservation based efforts.

Shortcomings of the survey include a lack of responses from some regions (such as the Northeast) and a lack of independent expert responses from some states. However, it provided the most comprehensive review that could be accomplished within a short time period of oyster resource status throughout the species range in the United States. The BRT believes this represents the most current information available to assist in evaluating the status of the species. The following is the analysis of the survey results.

Oysters were reported as "present" in nearly all estuaries.

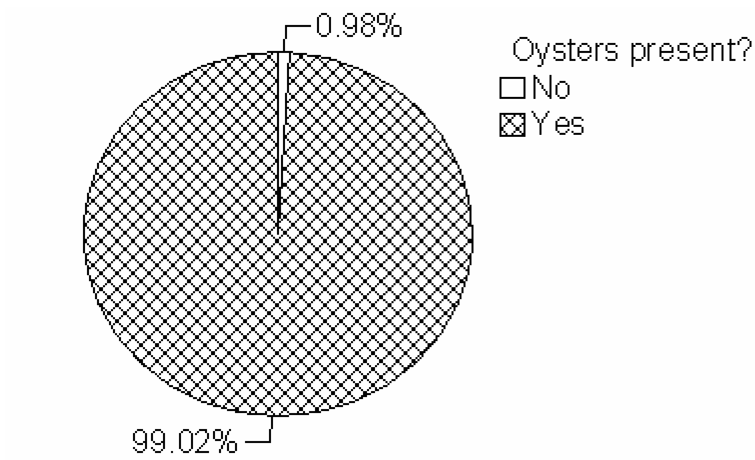

Figure 7. Response to the question: Are oysters present in the estuary?

Sixty-seven percent of estuaries support harvest, while 23% do not, and 10% have seasonal harvest.

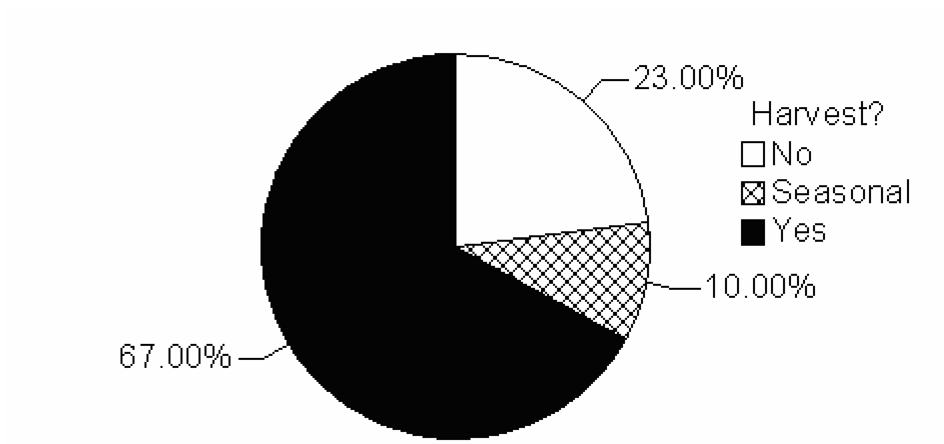

Figure 8. Response to the question: Does the estuary support harvest?

Based on fisheries-dependent data, respondents indicated that oyster populations are stable in 53% and unstable in 47% of the estuaries where they occur.

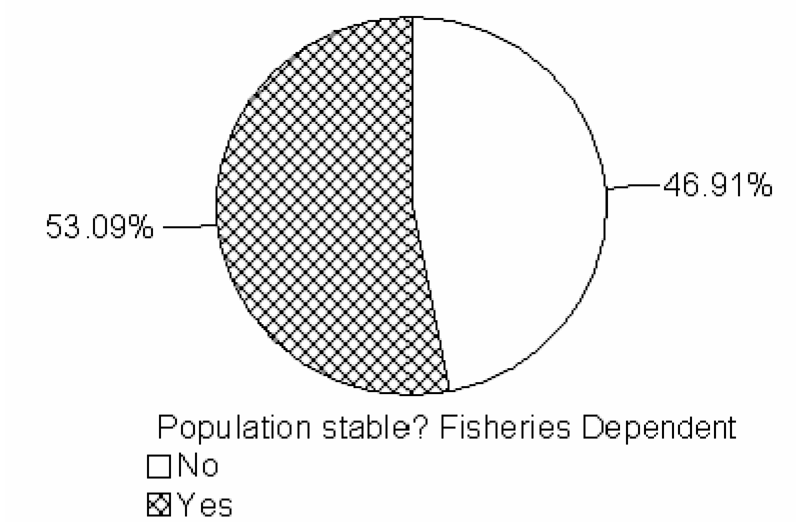

Figure 9. Response to the question: Based on fisheries dependent analysis, is the population stable?

Based upon fisheries-independent data, oyster populations were judged to be stable in 60% and unstable in 40% of the estuaries in which they occur.

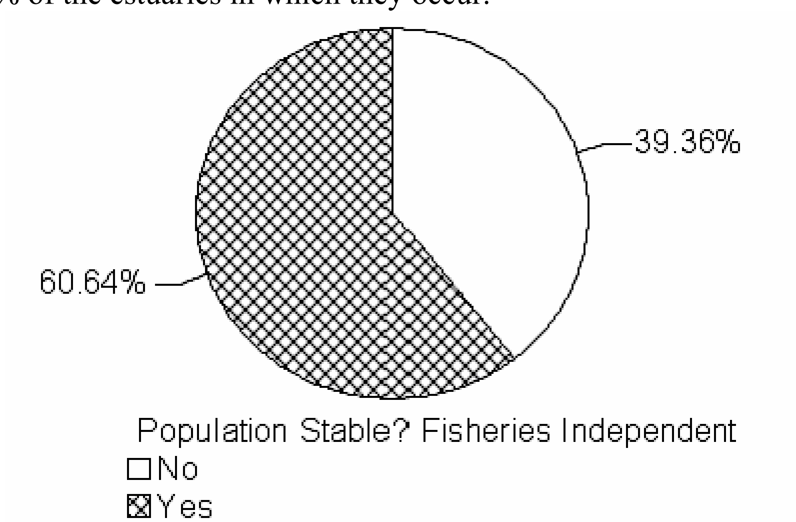

Figure 10. Response to the question: Based on fisheries independent analysis, is the population stable?

For the purposes of the survey restoration and enhancement were defined as follows:

Enhancement: the manipulation of the physical, chemical, or biological characteristics of a site to heighten, intensify or improve specific function(s). Enhancement results in a change in function, but not a change in acreage.

Restoration is an umbrella term that includes enhancement, creation and re-establishment. Creation is the manipulation of the physical, chemical or biological characteristics to develop oyster habitat where it did not previously exist. Re-establishment rebuilds oyster habitat where it once historically or formerly existed.

Over 80% of estuaries were thought to have sustainable populations in the absence of restoration and enhancement activities.

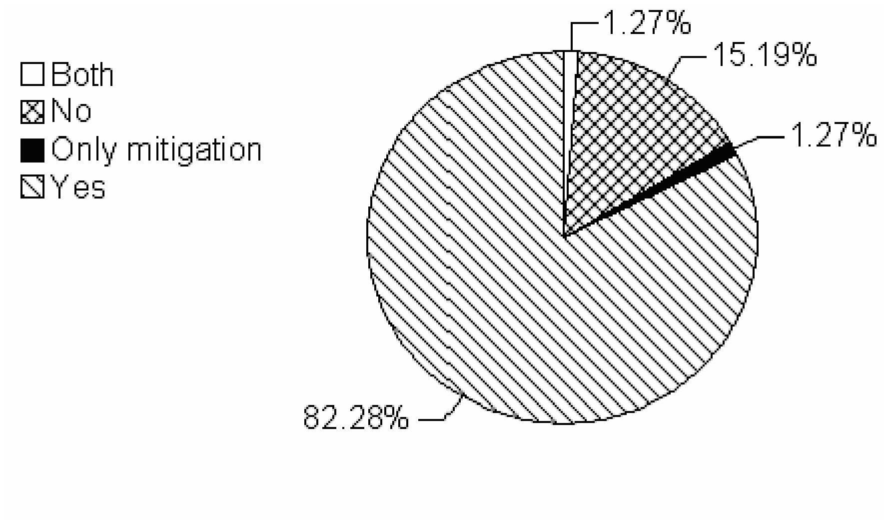

Figure 11. Response to the question: Is the population stable without restoration and/or enhancement?

Similarly, the proportion of estuaries thought to have sufficient recruitment is 81% and insufficient recruitment is 19%.

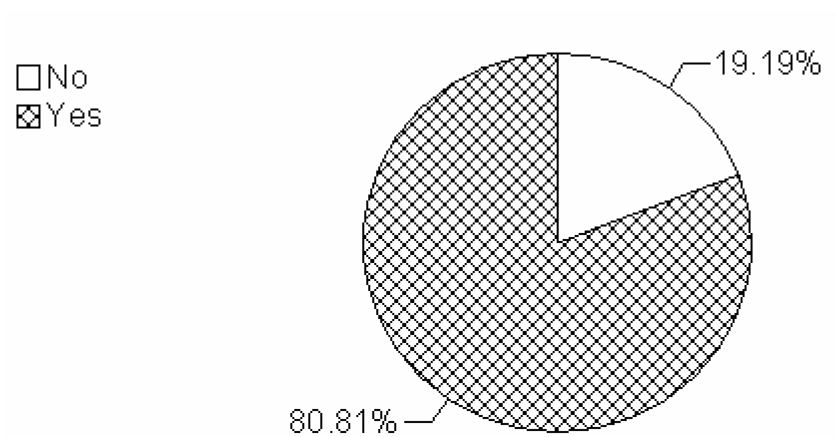

Figure 12. Response to the question: Is there sufficient recruitment?

Respondents reported that restoration and enhancement activities are occurring in 65% of the estuaries where oysters occur. Restoration and enhancement of oyster populations is associated with two main management goals, fisheries and conservation – often for both in the same estuary. There were no restoration or enhancement activities identified in approximately 35% of estuaries.

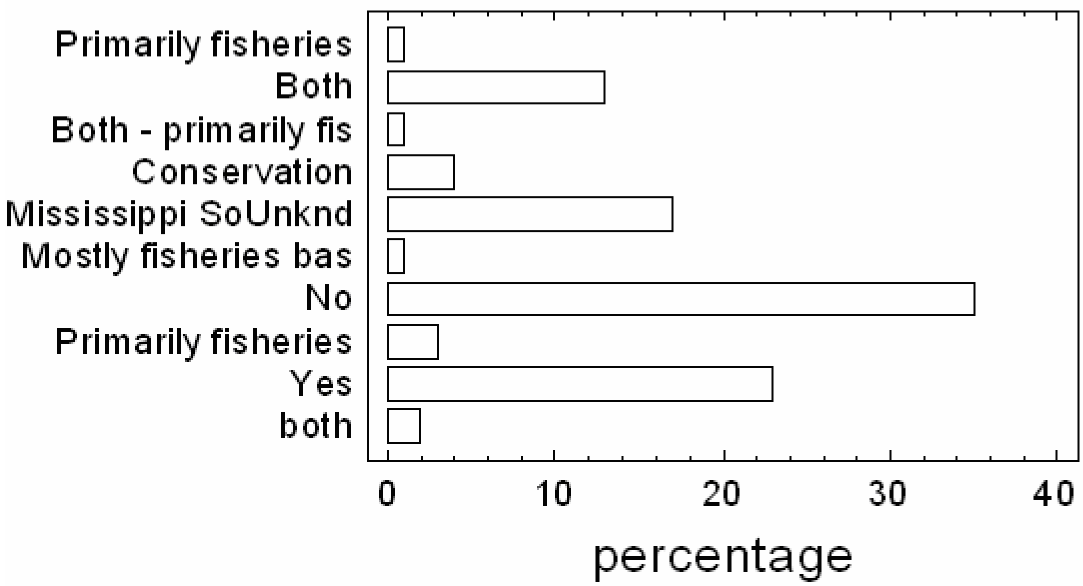

Figure 13. Response to the question: Is restoration or enhancement work conservation based or fisheries based?

The importance of diseases or parasites impacting oyster harvest was highlighted in roughly half of the estuaries.

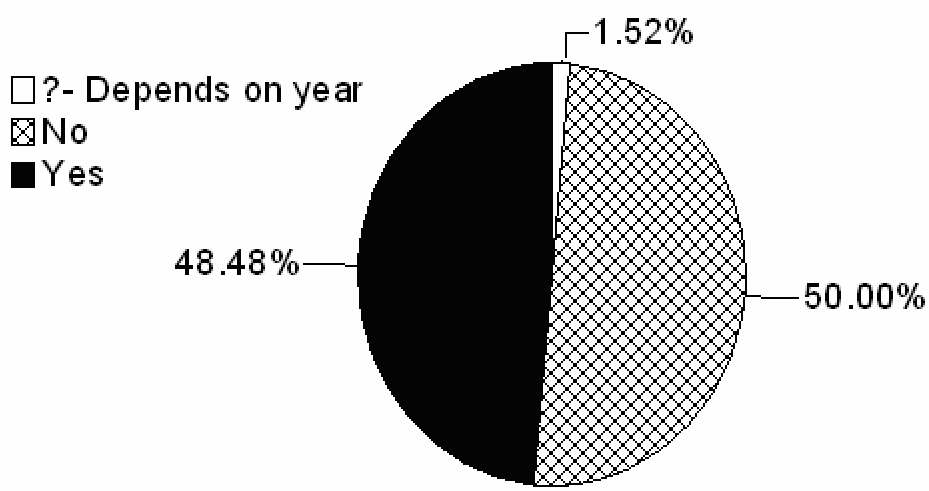

Figure 14. Response to the question: Is oyster harvest impacted by disease/parasites?

Possibly as a response to the threat of disease and parasite transfer, interstate transfer of oyster seed is widely regulated.

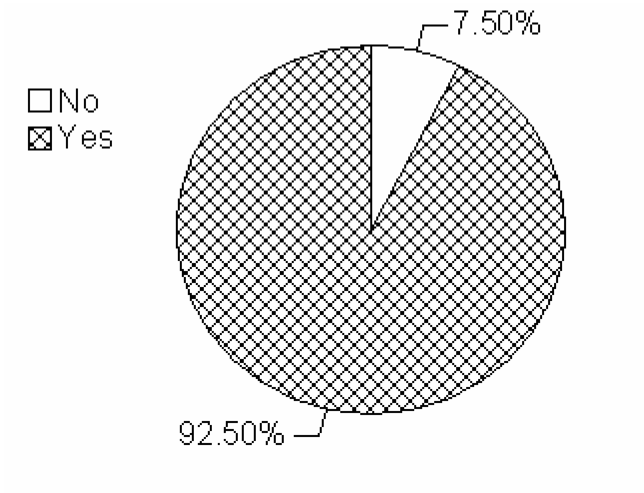

Figure 15. Response to the question: Is interstate transfer of oyster seed regulated?

Regulation within state boundaries of oyster seed movement was less-often subject to regulation.

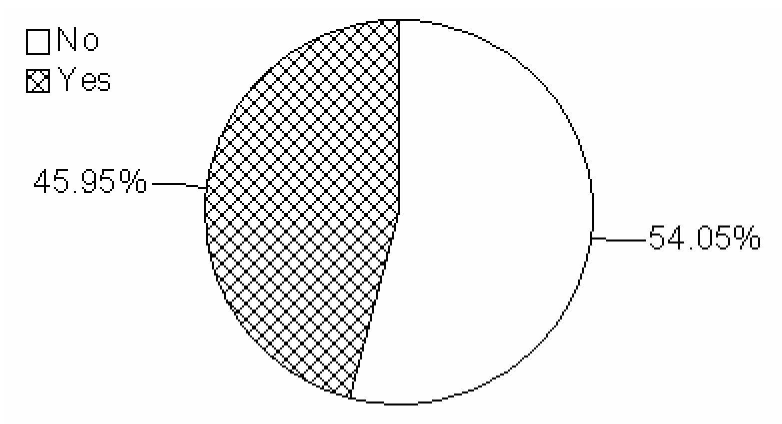

Figure 16. Response to the question: Is transfer of oyster seed within state boundaries regulated?

Harvest is regulated by both size and bag limit, with no limit in only 24% of estuaries reported.

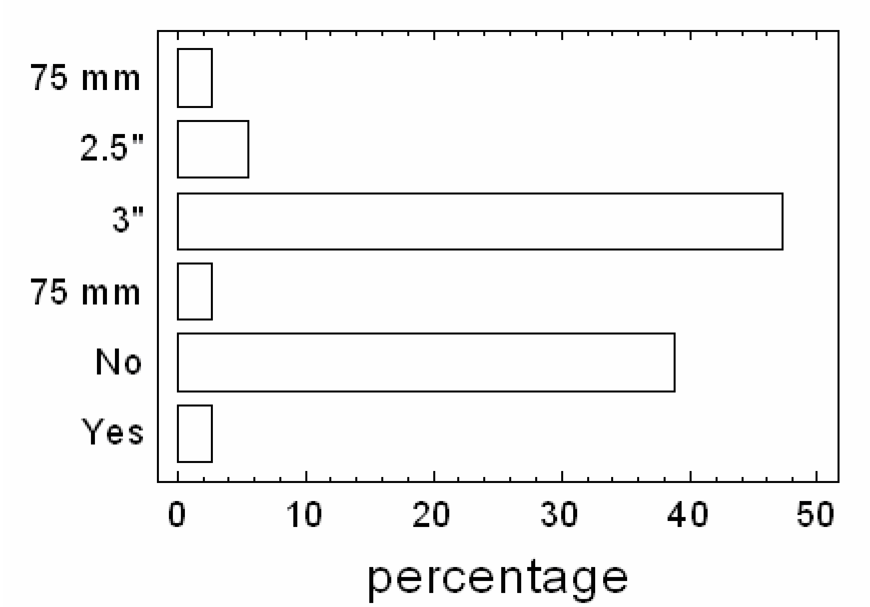

Figure 17. Response to the question: Is harvest regulation by size?

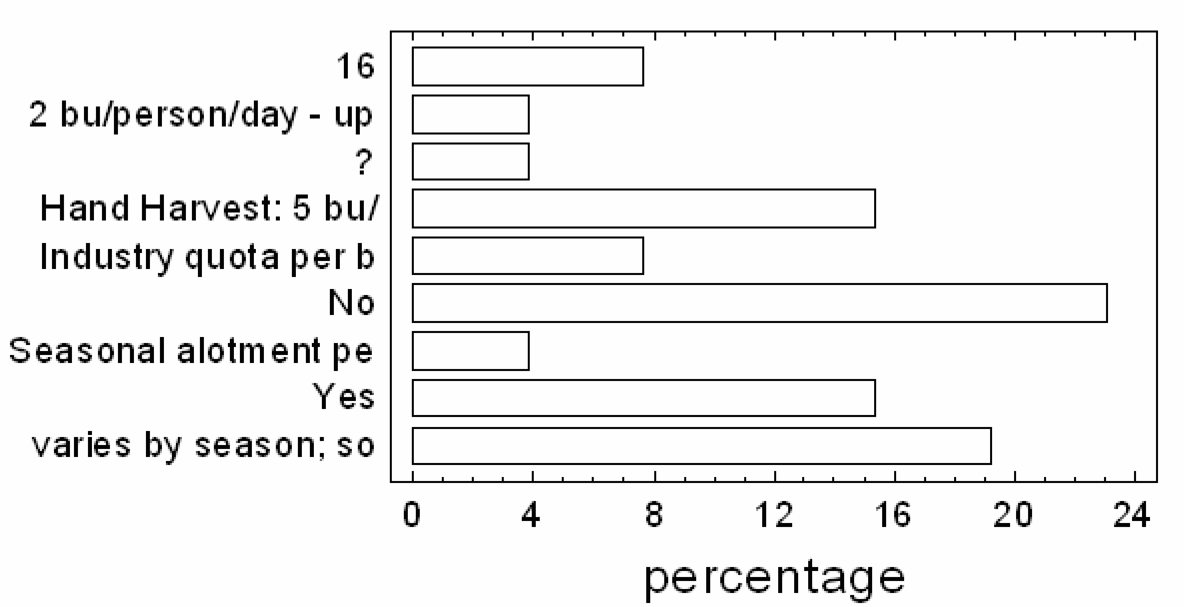

Figure 18. Response to the question: Is harvest regulation by bag limit?

Overall, shellfish managers felt that oyster populations are being successfully regulated in their estuaries.

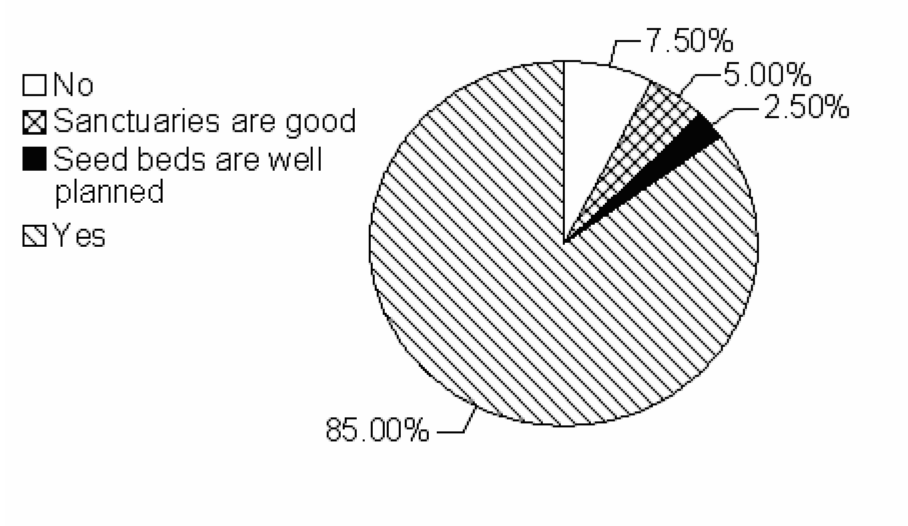

Figure 19. Response to the question: Are regulations sufficient?

	Recruitment Sufficient	Pop. Stable (Fishery-Indendent)	Pop. Stable (Fishery-Dependent)	Restoration	Sustainable without Restoration
Population stable (Fishery-Independent)	0.44 (0.016)				
Population stable (Fishery-Dependent)	0.31 (0.094)	0.30 (0.113)			
Restoration ?	-0.35 (0.054)	-0.47 (0.009)	-0.45 (0.012)		
Sustainable without Restoration ?	0.50 (0.005)	0.47 (0.009)	0.31 (0.096)	-0.43 (0.017)	
Regulation Sufficient ?	0.56 (0.001)	0.48 (0.007)	0.25 (0.178)	-0.35 (0.058)	0.73 (0.000)

Table 3. Matrix of correlations between responses to Survey questions relevant to population stability and sustainability (correlation coefficients and probability values in parentheses).

Significant correlations ($p<0.05$) reveal consistency in respondents' views of oyster populations in the estuaries for which they were reporting. In estuaries characterized as having sufficient recruitment, oyster populations were judged to be stable, by fisheries-independent criteria and sustainable without restoration, and regulations were judged to be sufficient to maintain oyster populations. In estuaries where oyster populations were thought to be stable, by fisheries-independent criteria, production was thought to be sustainable without restoration efforts, and restoration activities were less likely to be occurring than in estuaries with less-stable oyster populations. Similarly, in estuaries where oyster populations were judged to be sustainable by fisheries-dependent criteria, restoration activities were less likely than in estuaries with unsustainable fisheries. The strongest correlation obtained made the emphatic point that estuaries wherein regulation was sufficient were seen as sustainable without restoration.

In summary:

- Oysters are widely distributed and harvested throughout their range; they were reported to be currently present in all but one of the estuaries (Upper Laguna Madre);
- The surveys provided few data regarding historic and current oyster reef acreage estimates;
- Available fisheries dependent and independent data (e.g., long term quantitative stock assessments) are insufficient to assess stability of populations;
- Surveys strongly suggest that recruitment is sufficient to maintain the viability of the populations throughout its range except in a portion of the mid-Atlantic (e.g., Long Island Sound, Peconic Bay, Hudson-Raritan Estuary);
- Restoration and enhancement efforts for fisheries and conservation are occurring throughout the range, but are more common in the north and mid-Atlantic;
- In estuaries where restoration and enhancement efforts are occurring, they are considered necessary to sustain populations in roughly half of the estuaries in the mid and south Atlantic regions (presumably, to support commercially viable populations);
- In the North Atlantic (specifically, Connecticut and Rhode Island) and the Gulf of Mexico, restoration and enhancement efforts are not necessary to sustain biologically viable populations but are considered important to maintaining a fishery and conserving ecosystem services.

6.4 Extinction Risk Considerations

1) The species displays a wide range of survival strategies (i.e., it is both a colonizer and an ecosystem engineer, and has a high reproductive potential). The eastern oyster's ability to adapt to a wide range of environmental conditions (e.g. tolerance for low dissolved oxygen and wide ranges in salinity and temperature) makes the species resilient.

2) The species inhabits a naturally-variable environment; evidence is that past local extirpations and colonizations have been common over geologic time.

3) Threats are many, but none are overwhelmingly dominant or advancing at a rate that would threaten the viability of the species throughout its full range; however, there may be some threats that are significant at a regional or local level.

4) Fishery harvest declines, often cited as cause for alarm, are widely-recognized as unreliable indicators of population trends. Landings data are more a metric of fishery success rather than species abundance.

5) Restoration efforts for oysters are motivated by interest in reclaiming ecosystem services and/or sustaining fisheries, not by a perceived need to protect the species itself.

6) Domestication and farming of reproductively-isolated breeds of eastern oysters is expanding to satisfy market demand, with the ancillary benefit of moderating harvest pressure on natural populations.

7 Conservation actions

7.1 Past, Current, Anticipated Actions

Oyster reef restoration has been carried out since the late 1800's for the purposes of maintaining harvestable stocks of oysters. This work has historically been accomplished by oystermen and state resource managers. However in the last decade, restoration of oyster reefs has become the focus of a wide range of restoration practitioners interested in restoring oyster reefs for the purposes of conservation and provision of ecosystem services. While the goals of maintaining harvestable stocks of oysters and provision of ecosystem services are not necessarily mutually exclusive, the scale, techniques and funding associated with the two types of restoration are very different.

The history of oyster restoration through the late 1990's has been summarized by Luckenbach et al. 1999. Case studies included in this compilation summarize the main goals of oyster reef restoration. Besides the small scale efforts by oystermen in the late 1800's and early 1900's to replace oyster shell harvested from reefs, most oyster restoration has historically been managed by the states. The focus of these restoration efforts has been to maintain or increase oyster habitat through placement of cultch in areas where commercial harvest has been successful. The loss of cultch typically resulted from harvest or natural disaster.

Many cultch materials and placement techniques have been used with varying degrees of success. Cultch materials have included harvested oyster shell, *Rangia* clam shell (often mined), crushed limestone, crushed concrete, gypsum fly ash, calico scallop shell, and fossilized (mined) oyster shell. Most state managed efforts have focused solely on the placement of cultch materials; however, a few small-scale efforts have also included dispersal of oyster seed (small juvenile oysters). Dispersal of cultch material was historically contracted to oystermen using their own boats but much of the larger scale work is now done by blowing cultch off barges with high pressure water cannons.

Funding has been provided for oyster reef restoration focused on maintenance of commercially harvested reefs through a number of sources, including taxes placed on harvested oysters. Federal relief following natural disasters such as hurricanes has also provided a large source of funds for areas in the northern Gulf of Mexico. For instance, following Hurricane Ivan in 2004, Federal relief funding in the amount of $9 million dollars was divided between the states of FL, AL, MS and LA for the purposes of oyster reef restoration. Most states also provide funding to support continuous and on-going restoration efforts and some states have also enacted laws to ensure that harvested oyster shell is returned to the state for restoration projects.

It is difficult to estimate the number of acres that have been restored for the purposes of commercial harvest. Each state manages very unique programs with funding levels varying greatly between years. However, it can be easily concluded that state resource managers typically support restoration projects of a much larger scale than projects done for the purposes of conservation and ecosystem services. For instance, the State of Alabama has proposed to rehabilitate approximately 1,800 acres of “prime oyster bottom” through placement of cultch over a three year period beginning in 2005; whereas, oyster reef restoration for the purposes of conservation in Alabama have totaled less than 5 acres over the last 4 years. Louisiana also regularly plants cultch material on public oyster bottoms, with the most recent being the planting of nearly 250 acres in the spring of 2003. Since 1919, Louisiana has planted over one million cubic yards of cultch material on public water bottoms.

As stated previously, in the last decade many restoration practitioners have come to support oyster restoration efforts for the purposes of conservation and provision of ecosystem services. Specifically, construction of oyster reefs is supported as an avenue for protecting biodiversity, regulating nutrients in estuaries through water filtration, protecting shorelines from erosion, and providing habitat for many estuarine species. Restoration projects accomplished with these goals in mind typically do not promote oyster harvesting on the restored reefs.

A number of groups are now involved in oyster restoration with these goals in mind including state resource managers, non-profit “environmental” groups, colleges and National Estuary Programs. Projects of this type typically involve the local community through volunteer activities, education and/or outreach and scientific monitoring. In fact, many of these projects are scientifically monitored with the goal of gaining a better understanding of the numerous ecosystem services provided by oyster reefs. The hope is that more completely understood and quantified ecosystem services will result in a stronger argument for increased funding and support for these types of oyster restoration efforts.

Cultch materials used for these types of restoration projects are similar to those used for restoration of commercial reefs, including fossilized oyster shell, harvested oyster shell, marl rock and concrete rubble. However, a variety of techniques are used for deployment based on the size/scale of the project. For instance, the South Carolina Oyster Restoration and Enhancement (S.C.O.R.E.) program typically creates reefs that are less than 0.1 acre in size by utilizing volunteers to collect discarded oyster shell from local seafood restaurants. Once the shell has dried in open-air bins, volunteers then place the “recycled” shell into mesh bags and deploy them along tidal creek shorelines to provide settlement area for oyster larvae. On the other hand, restoration in the Chesapeake could be categorized as both small scale (typically one acre or less) and large scale (typically greater than 5 acres). Small-scale projects have included planting shell in various thicknesses and in three-dimensional piles, experimenting with various alternative substrates (stone, marl, slag, concrete rubble, concrete forms, coal fly-ash, porcelain, surf clam shell, and ocean clam shell), various planting densities, and various oyster “strains” for disease tolerance performance. Large-scale projects typically include some combination of the following: a) "bar-cleaning" of remnant sites to remove old, potentially diseased oysters and sometimes to remove silt; b) planting of additional shell substrate (where needed); and c) re-planting with hatchery-produced spat-on-shell (in areas where natural spatset is not likely or occurs infrequently).

Grant funding is a common mechanism used to accomplish oyster restoration for the purposes of conservation and ecosystem services. Federal monies appropriated through NOAA are likely the largest source of such funds available on a nationwide basis. For instance, in 2005 the NOAA Restoration Center awarded $8.9 million through the Community-based Restoration Program (CRP) to support marine and anadromous fisheries habitat restoration projects. However, given the competitive nature of the funding assistance program, only a portion of the available funds will be used to support oyster restoration projects in any given year. Of the more than 900 projects NOAA has supported since 1996, approximately 10% have benefited the eastern oyster.

In the Chesapeake Bay area, the U.S. Army Corp of Engineers is also a significant source of funding for oyster restoration efforts. Since 2002, USACE funding has been on the order of $3 million dollars per year, for restoration activities in Maryland and Virginia waters. The Maryland portion of these funds has targeted reconditioning reefs via placement of additional shell layers on historic oyster bottom. These sites are then typically seeded with hatchery produced disease-free seed oysters, produced at the University of Maryland hatchery facility with funds provided by the state of Maryland and NOAA (implemented through the Oyster Recovery Partnership). In Virginia, efforts have focused on developing tributary-intensive restoration plans, whereby large portions of the historic oyster bottom are reconditioned with shell, and smaller areas are densely seeded with specific genetic strains of oysters in the hope of developing a localized disease-resistant population.

Estimates of the acreage of oyster reef restored for conservation have been calculated based on the assumption that the majority is supported through the NOAA and USACE programs described above. NOAA Restoration Center administers a number of programs and funding mechanisms, including the CRP (mentioned above), Directed Appropriations, and the Damage Assessment and Restoration Program. The CRP granting program has supported the restoration of more than 74 acres of oyster reef from Maine to Texas, the vast majority of which does not experience harvesting pressure. Through Directed Appropriations, funds appropriated through Congress for specific local programs and projects, the Restoration Center has supported more than 1,034 acres of oyster reef restoration. An additional 16.5 acres of oyster reef restoration has been accomplished through the Damage Assessment and Restoration Program, whereby NOAA acts on behalf of the public to restore natural resources injured by hazardous spills or groundings. Since 1992, it is estimated that the USACE has supported the restoration of approximately 80 acres of oyster reef each year. While the acreage associated with these projects appears substantial, it should be clarified that the vast majority of the NOAA effort has been focused on the Chesapeake Bay including 40 of the 74 acres of oyster reef restored by the CRP and more than 680 of the 1,034 acres restored through Directed Appropriations. Also, given the fact that NOAA and the USACE often support different aspects of the same oyster restoration project, it is not possible to simply add the NOAA acres with the USACE acres to determine an overall acreage of oyster reef restored in the Chesapeake. Adding the two acreage estimates together would greatly overestimate the numbers of acres restored.

Another difficulty in determining the effects of oyster restoration on the status of the species results from the fact that individual projects have vastly different success criteria; therefore, an acre of “restored” oyster reef does not always equate to an acre of oyster reef restored to full function. Even if full function had been achieved on all 1,124+ acres of restored oyster reef, it would be difficult to argue that these actions have had a measurable impact on the status of the eastern oyster species throughout its range.

There are several major weaknesses associated with oyster reef restoration done for the purposes of conservation and ecosystem services. The first two of these are closely associated with the grant funding process. First, is a lack of long term scientific monitoring to evaluate project success. While most projects are subject to some degree of monitoring during the early months following restoration, funds are typically not available to monitor the restored reefs through time. This artifact of the grant mechanisms, which typically awards funds for a 1-2 year period, results in a lack of long-term knowledge about the effectiveness and long-term sustainability of such efforts. Second, is a lack of large-scale restoration projects to truly test the effectiveness of oyster restoration for the purposes of ecosystem services. It is simply not possible to quantify the water quality improvement in the Chesapeake Bay resulting from a 0.5 acre restoration project. Therefore, arguments to increase funding and public interest in oyster restoration focused on conservation are more difficult to fully support. Small scale efforts are an artifact of the grant process due to range of awards provided. For instance, the Restoration Center encourages projects to apply for funding in the range of $35,000 to $250,000. Only a few projects can be awarded funding in the higher range due to the limited amount of funding available for all project types so large scale projects are unachievable on the small budgets available. The third weakness identified is a lack of wide-ranging support from state resource managers and state regulations. Most state resource managers must follow statutes that only considered restoration for the purposes of commercial harvest. They are often limited in their ability to pursue and encourage restoration in areas that are not open for harvest.

In 2003, the NOAA National, Maryland and Virginia Sea Grant Programs brought together scientists, resource managers, and industry representatives from across the nation to prioritize key research areas for restoration of oyster resources. Developing populations of oysters better able to survive MSX and Dermo was identified as a high priority (UM-SG-TS-2004-02, VSG-04-01). Several disease resistant strains are under development and two, the Haskin CROSBreed and Andrews DEBY lines, are available for commercial production (Allen et al. 2003). These selected lines are widely recognized as good candidates for aquaculture operations due to their initial disease resistance and fast growth but they may not be sufficient for restoration of wild populations because they may not survive long enough to produce disease resistant progeny (UM-SG-TS-2004-02, VSG-04-01). It is also currently unknown if these disease resistant traits can be transmitted to the natural population (Allen et al. 2003, Angione 2005). Hatchery production might be a genetic bottleneck if supportive breeding is not properly carried out (Allen and Hillibish 2000). Despite concerns about decreasing genetic variability through hatchery propagation, regional scientific groups initially advocated large scale seeding of Chesapeake Bay reefs with these disease resistant stocks (Allen et al. 2003). More recently, however scientific guidance has recommended against this due to evidence that beneficial traits may not pass to intermixed (native and specific-strain) offspring. Disease resistant stocks have been used in small scale public oyster restoration programs sponsored by Maryland’s Oyster Recovery Partnership, the Chesapeake Bay Foundation, and the US Army Corps of Engineers in Chesapeake Bay (Allen et al. 2003). Research is underway to establish the molecular genetic profile for these disease resistant oysters. This profile can be identified in subsequent generations, and will indicate the degree to which the selectively bred broodstock contribute progeny to the next generation of oysters (Allen et al. 2004).

8 Research Needs

8.1 Gaps in Knowledge/Future Needs

1) Fishery independent surveys
2) Further genetic analysis of population structure with a focus on local or regional adaptations
3) Research on proximity-recruitment relationship
4) Research on effects of combined and chronic stresses including changes due to future climate change
5) Continued research on disease susceptibility and development of selectively bred disease tolerant strains
6) Emerging role of endocrine disruptor pollutants upon population biology
7) Delineation of oyster habitat
8) Compatibility of information
9) Continued ecological risk associated with other oyster or other alien species introductions
10) Control and abatement of threats from all sources
11) Develop a standardized monitoring protocol at a local or regional level
12) Research on the effects of changes in coastal development and demographics.

9 Conclusion

Based on the available information, the BRT concludes that the long term persistence of eastern oysters throughout their range is not at risk now or in the foreseeable future. This completes the BRT's evaluation of the status of eastern oysters throughout their range. This comprehensive status review, as compiled and deliberated by the BRT, incorporates and summarizes the best available scientific and commercial data to date.

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Appendix I. Glossary of Terms

Allele- An alternative form of a given gene that differs from other alleles in DNA sequence or in effect on phenotype.
Allele frequency- The percentage of all alleles at a particular locus represented by a particular allele in the gene pool of a given population.
Allozyme- Allelic form of an enzyme encoded at a given locus. Allozymes usually are distinguished by electrophoresis and histochemical staining and are observed as a difference in electrophoretic mobility due to differences in net electric charge or molecular weight.
Balancing selection- A type of natural selection in which a diversity of alleles is maintained by the changing action of selection in a dynamic environment.
Cline- A gradual spatial variation in allele frequencies exhibited by a species along a line of environmental or geographic transition.
Directional selection- A mode of selection favoring phenotypes at one end of the population's phenotypic distribution.
Denaturing Gradient Gel Electrophoresis (DGGE)- A molecular technique that works by applying DNA (or RNA) to an electrophoresis gel that contains a denaturing agent. Certain denaturing gels are capable of inducing DNA to melt at various stages. Sequence differences in otherwise identical fragments often cause them to partially melt at different positions in the gradient and therefore stop at different positions in the gel. By comparing the melting behavior of the polymorphic DNA fragments side-by side on denaturing gradient gels, it is possible to detect fragments that have mutations in the first melting domain. Placing two samples side-by-side on the gel and allowing them to denature together, researchers can easily see even the smallest differences in two samples or fragments of DNA. Similar to SSCP.
Ecosystem services- Protection of biodiversity; regulation of nutrients in estuaries through water filtration; protection from shorelines erosion; provision of habitat for many estuarine species.
Effective population size (N_e)- The number of reproducing individuals in an ideal population that would lose genetic variation due to genetic drift or inbreeding at the same rate as the number of reproducing adults in the real population under consideration. Typically, N_e is less than either a population's total number of sexually mature adults present or the total number of adults that reproduced. Effective population number can be defined either in terms of the amount of increase in homozygosity (inbreeding effective number) or the amount of allele frequency drift (variance effective number).
Electrophoresis- A procedure for separation of charged molecules in an electric field, for example, for screening of allozyme variation. Refers to the electromotive force (EMF) that is used to push or pull molecules through the gel matrix; by placing the molecules in wells in the gel and applying an electric current, the molecules will move through the matrix at different rates, towards the anode if negatively charged or towards the cathode if positively charged (note that gel electrophoresis operates as an electrolytic cell; the anode is positive and the cathode is negative).
Enhancement- the manipulation of the physical, chemical, or biological characteristics of a site to heighten, intensify or improve specific function(s). Enhancement results in a change in function, but not a change in acreage.

Fixation Index (F_{st})- The proportion of the variation at a locus attributable to divergence among populations. Measures the reduction in total expected heterozygosity of the entire system of populations due to random drift and other differentiating processes among isolated populations.
Gel- The matrix used to separate the molecules. When separating proteins or small nucleic acids (DNA, RNA, or oligonucleotides) the gel is made with different concentrations of acrylamide and a cross-linker, producing different sized mesh networks of polyacrylamide. When separating larger nucleic acids (greater than a few hundred bases), the preferred matrix is purified agarose (which is a seaweed extract). In both cases, the gel forms a solid but porous matrix that looks and feels like clear jello.
Gel electrophoresis- A group of techniques used by scientists to separate molecules based on physical characteristics such as size, shape, or isoelectric point. Gel electrophoresis is usually performed for analytical purposes, but may be used as a preparative technique to partially purify molecules prior to use of other methods such as mass spectrometry, PCR, cloning, DNA sequencing, or immuno-blotting for further characterization.
Genetic distance- An estimation of the number of allelic substitutions per locus that have occurred since separation of a population pair.
Genetic drift- Random changes in allelic frequencies that occur in each generation due to natural sampling errors. The rate of genetic drift increases as effective population size decreases.
Gene flow- Genetically effective migration; the movement of genes among populations of a species.
Genetic marker – A genetic factor (e.g., a gene or other identifiable portion of DNA) or gene product that results from random mutations in the DNA sequence which act as genetic milestones. An observable characteristic useful for genetic analysis.
Haplotypes- A specific mitochondrial DNA pattern or a collection of co-inherited nuclear DNA alleles or markers.
Hardy-Weinberg Equilibrium- A model that predicts that for genetic characters the frequency of alleles remains constant from one generation to the next so long as the organisms are diploid, reproduce sexually, mate randomly, and the population is not subject to mutation, migration, or selection.
Locus-The site that a gene or molecular sequence of interest occupies on a chromosome (plural is **loci**-multiple genes of interest).
Mitochondrial DNA (mtDNA)- A small proportion (<1%) of the DNA of eukaryotic cells that is nonnuclear, located within organelles in the cytoplasm called mitochondria, and appears to have been endosymbiotic in early eukaryotic cells, as its genetic code differs from the "universal" genetic code. Animal mtDNA is a double-stranded, circular molecule usually ranging in size from 14,000 to 26,000 bp.
Panmictic- Well mixed, referring to the set of genotypes in a population.
Polymorphism- Multiple alleles of a gene within a population, usually expressing different phenotypes.
Polymerase Chain Reaction (PCR)- A molecular biological technique for amplifying (creating multiple copies of) DNA without using a living organism, such as *E. coli* or yeast. The technique allows a small sample of DNA to be copied multiple times so it can be used for analysis.
Restoration- an umbrella term that includes enhancement, creation and re-establishment. Creation is the manipulation of the physical, chemical or biological characteristics to develop oyster habitat where it did not previously exist. Re-establishment rebuilds oyster habitat where it once historically or formerly existed.

Restriction enzymes- An enzyme that cleaves DNA molecules at specific recognition sequences; for example, the enzyme *Alu I* cuts DNA at the sequences AG↓CT. In the producing organism, restriction enzymes are a defense against foreign DNA. In molecular genetics, they are utilized in cloning and population genetic analysis.
Restriction Fragment Length Polymorphism (RFLP)- Variation in the length of DNA fragments generated within a species when treating longer DNA segments with a restriction enzyme. The variants may be due to differences in DNA sequence at the recognition site where cleavage occurs (i.e., the enzyme does or does not cut) or to variations in length of the cleaved segment (often due to presence of varying members of tandem repeat motifs).
Secondary structure- The helical, or twisting, appearance of the DNA (or protein) molecule.
Single Nucleotide Polymorphism (**SNP)**- DNA sequence variation, occurring when a single nucleotide: adenine (A), thymine (T), cytosine (C) or guanine (G) - in the genome is altered. For example, a SNP might change the nucleotide sequence AAGC**C**TA to AAGC**T**TA. A variation must occur in at least 1% of the population to be considered a SNP.
Single-Strand Conformational Polymorphism (SSCP)- A molecular technique based on the concept that single stranded DNA form unique secondary structures and that the secondary structures are dependent on the sequence. A single base substitution may create different secondary structures. PCR-amplified DNA is denatured and run on a gel, and single stranded DNA with different secondary structures will have different mobility on the gel. Similar to DGGE.

Appendix II. Survey Form

Resource Managers Eastern Oyster Survey

One questionnaire will be completed for each estuarine complex or Shellfish Growing Area (SGA) in the state. (Only one section on regulations will be completed unless they vary between SGAs.)

State________

Based on the 1995 National Shellfish Register of Classified Shellfish Growing Waters, how many SGAs are in this state?____

Is there significant oyster acreage in your state unaccounted for in the Shellfish Register?

Yes___ Estimate # acres_____ No____

Notes____

____

Name of estuary/ SGA ______________________________

1. **Are oysters present in this estuary/SGA? Yes_____ No _____ Unknown _____**
2. **Does oyster harvest take place in this estuary/ SGA? Yes _____ No _____**
3. **What percentage of reefs are in harvestable areas? _____% unknown _____**
4. **Is harvest allowed? Seasonal ___Year round _____ Not applicable____ Usual Season ____**
5. **Is your population estimate within the estuary/SGA stable based on <u>fisheries dependent</u> data? Yes _____ No _____ Unknown _____**
   Stable based on <u>fisheries independent</u> data? Yes____ No____ Unknonwn____

Notes____

____

6. **Does sufficient recruitment take place within the estuary/SGA to sustain the viability of the population? Yes _____ No _____ Unknown _____**

Notes____

____

7. **Has oyster restoration or enhancement work been done in this estuary/SGA? Yes _____ No _____ Unknown _____**
   If yes, is it conservation based or fisheries based? _______________
   If yes, would the population sustain itself without restoration efforts? Yes____ No___ Unknown____

Notes____

____

8. **Do disease or parasites put the sustainability of harvested oysters at risk? Yes _____ No _____**
9. **Do disease or parasites put the sustainability of non-harvested oysters at risk? Yes __No _____**
10. **Do you have an estimate of "historic" total oyster acreage for this estuary/SGA or for the entire state? Yes _____ #acres _____ No _____**

Notes____

____

11. **Do you have an estimate of current total oyster acreage for this estuary/SGA or for the entire state? Yes _____ #acres _____ No _____**

Notes____

____

Threats to oyster populations

1. What, if any, do you perceive as the primary threats to the oyster population in this estuary/SGA? (i.e. Habitat Threats; Overutilization threats; Predation & Disease threats; Regulatory threats; Other natural or manmade threats) Explain.

Notes____

____

____

Regulations (*Please request an electronic copy or website for state regulations)

1. Does your state have harvest gear size and type restrictions? Explain

____

____

2. Are private leases allowed in your state? Yes _____ No _____

3. What is your states total lease acreage? _____# of acres or _____% of total.

4. What is your states total harvestable public acreage? _____# of acres or ______% of total.

5. Do you allow seeding of private leases from public reefs? Yes _____ No _____

6. Is there a minimum oyster size limit? Yes _____ No _____ What is it? _____

7. Are there daily sack limits on public reefs? Yes _____ No _____

Notes____

8. Do you feel that current regulations are sufficient to sustain oyster populations? Yes _____ No _____

Notes____

____

9. Does your state regulate the amount of shell or cultch material that must be returned to the estuary after harvest? Yes _____ No _____

Notes____

____

10. Does your state have regulations for <u>inter-state</u> oyster or seed transport/transplant? Yes____ No_____ If so, are they adequately enforced? Yes____ No____

Does your state have regulations for <u>intra-state</u> oyster or seed transport/transplant? Yes____ No____ If so, are they adequately enforced? Yes____ No____

Notes____

____

Survey completed by: ________________ ___________________

Agency/Organization_____________Title: ___________________

Phone # ____________________E-mail:____________________

Biological Review Team Member: ___________ _____________

Date: ______________

Survey # _____ of _____ for State _____

Appendix III.

This table shows each state and the number of estuaries/ SGAs for which responses were sought on the survey. It also shows if responses were successfully obtained from both a resource manager and an independent expert.

State	# estuaries/ SGA	Resource Manager (Y/N)	Independent Expert (Y/N)
Alabama	2	Y	Y
Connecticut	1	Y	N
Florida	24	Y (for 24)	Y (for 6)
Georgia	8	Y	Y
Louisiana	8	Y	Y
Maine		N	N
Massachusetts		N	N
Mississippi	1	Y	N
Maryland	1	Y	N
New Hampshire		N	N
North Carolina	2	Y	Y
New Jersey	2	Y (for 2)	Y (for 1)
New York	4	Y	Y
Rhode Island	3	Y (for 3)	Y (for 1)
South Carolina	7	Y	N
Texas	8	Y	N
Virginia	1	Y	N